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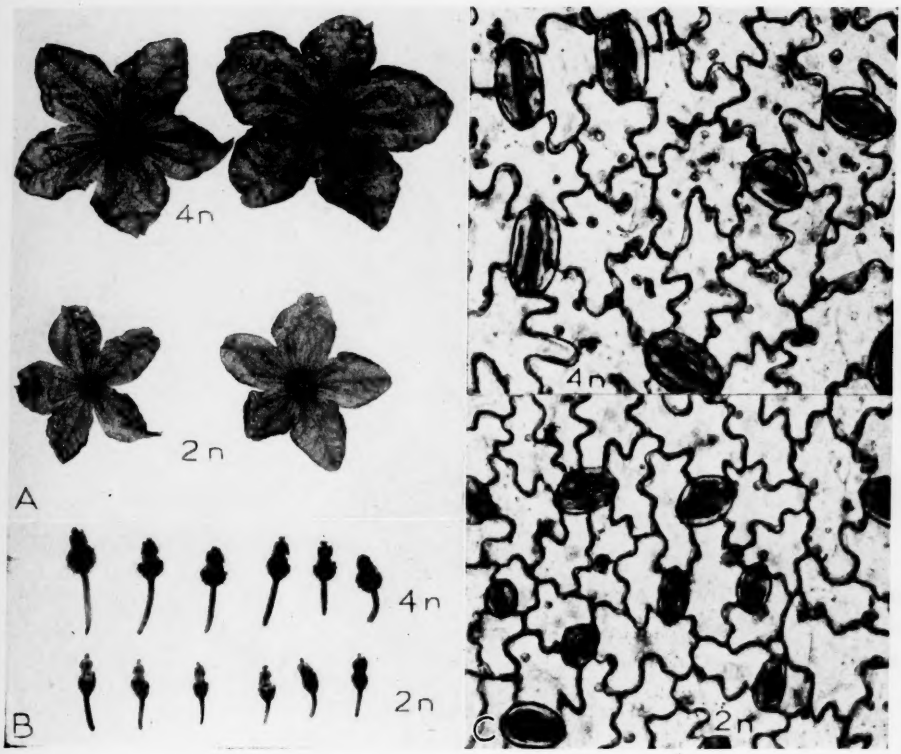

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Detection of Linkage in Man
The "Aryan Breeding" Industry
An "Auto-Sexing" Variety of Pigeon
Structure of Salivary Gland Chromosomes
Coat Color and Temperament in the Ground Squirrel

VOLUME 33 APRIL, 1942 NUMBER 4

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The

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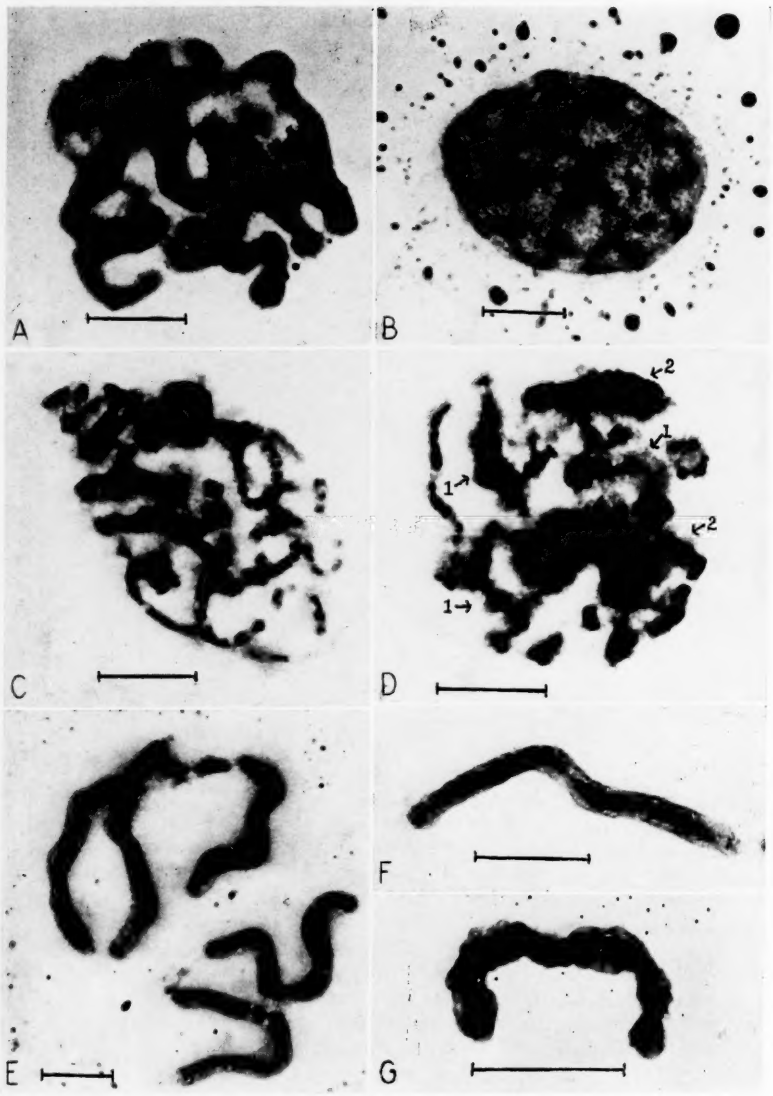

STAGES IN THE TRANSFORMATION OF CHROMOSOMES

Figure 1

Microphotographs of various stages in the appearance of chromosomes when acted on by urea-alkali solutions. These changes are shown schematically in Figure 4. The stages shown here are in the alpha (α) and gamma (γ) series: *A*—α_1; *B*—α_0; *C*—γ_1; *D*—γ_2 and α_3; *E*—γ_3; *F*—γ_{2-3}; *G*—β. All scales are 10μ.

THE STRUCTURE OF THE SALIVARY GLAND CHROMOSOMES

Of *Drosophila Melanogaster*

II. Effects of Urea-Alkali Mixture and Other Chemicals on the Structure of Salivary Gland Chromosomes

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A BRIEF account of the process of the transformation of the salivary gland chromosomes from the normal structure to the lampbrush and other types by treatment with an alkali was presented in a previous publication.[5] It was noticed then, though not mentioned in that paper, that a simple *1 N* solution of sodium hydroxide (NaOH) sometimes fails to produce the typical lampbrush chromosomes. Since a perfectly reliable reagent was desirable for further studies of the phenomenon, a search was made for some chemical which would produce the lampbrush chromosomes in all chromosomes treated or one which would improve the action of the alkali. Of a number of organic and inorganic bases which were studied none was as effective as the NaOH, but urea, potassium cyanide (KCN) and acetamide were found to improve the action of the NaOH. With the NaOH improved by addition of urea the processses of transformation have been reinvestigated. The details of the investigation will be presented in this paper and on the basis of the results of this investigation the structure of normal salivary gland chromosomes will be interpreted.

Reagents, Material and Technique

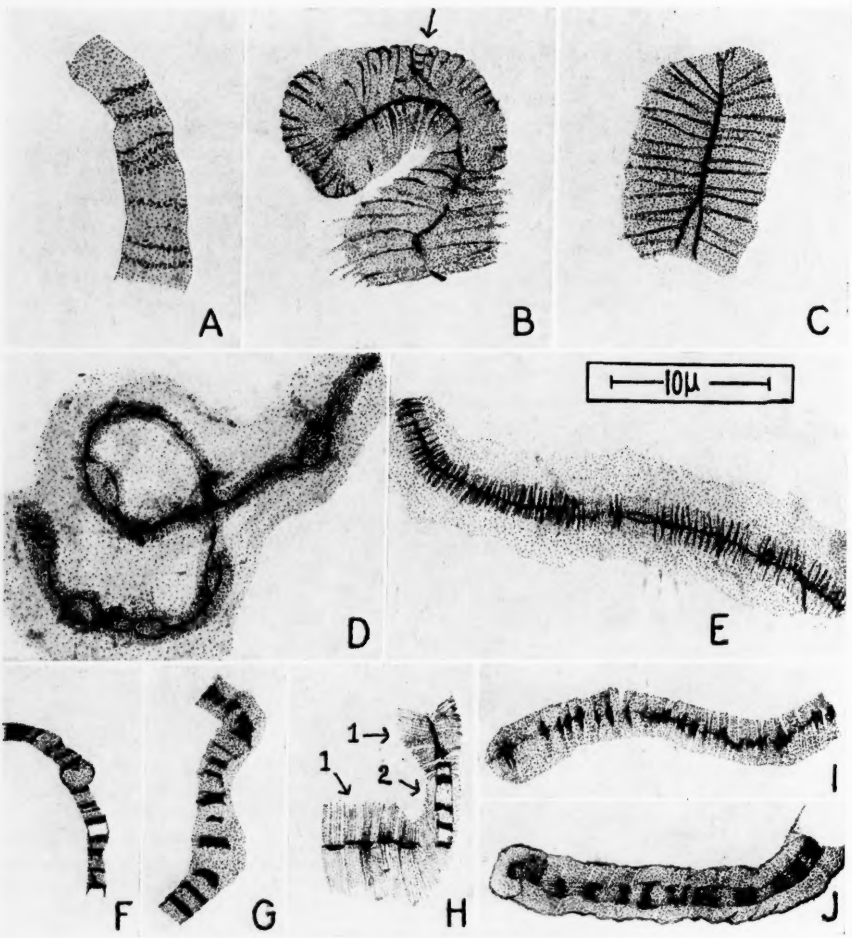
The stock solution from which the reagents were made is prepared by mixing equal amounts of *1 N* NaOH and saturated aqueous solution of urea made by the dissolving of 120 grams of urea in 100cc. of water. The urea solution is warmed before use if the urea crystals are not completely dissolved. The stock solution, which will be called the "standard mixture," should be used as soon as it is prepared. The mixtures used for the present studies are 50%, 30% and 10% aqueous solutions of the standard mixture. These mixtures are also to be used as soon as they are prepared

The salivary glands dissected from fully mature larvae of *Drosophila melanogaster* are treated in a few drops of mixture on a slide for a desired length of time. The glands are more or less completely dissolved during treatment, especially if the treatment is long. Therefore, many glands should be treated simultaneously, so that enough material will remain visible at the end of the treatment. The treated glands are stained and smeared with acetocarmine. In special cases where the details of certain structures do not show up in the acetocarmine preparation, Delafield's haematoxylin has been used according to the following procedure: The treated glands are fixed with a 45% aqueous solution of acetic acid for about ten minutes and smeared. After dehydration in an alcohol chamber over-night the cover glass and the slide are hydrated, stained with Delafield's haematoxylin, dehydrated and sealed with balsam. Other technical methods will be described as they come into discussion in the subsequent sections.

Determination of Transformation Series

In the previous paper[5] two types of transformation, each with a small number of stages, were described. The pres-

*The author is greatly indebted to Professor R. B. Goldschmidt under whose guidance this series of investigation is in progress. The publication of the extensive series of photographs and drawings has been made possible through a grant for this purpose from the Research Fund of the University of California.



ALPHA AND GAMMA TRANSFORMATIONS

Figure 2

Camera-lucida drawings of various stages of α- and γ-series. *A*—*A*-stage; *B*—α_2 (arrow points to a "finger-like body"); *C*—the nucleic acids of the finger-like bodies are partly dissolved; *D*—α_{2b}; *E*—α_3, showing organization of diffused nucleic acids into hairs; *F*—γ_1; *G*—γ_2; *H*—$\gamma_2(2)$ and $\alpha_3(1)$ are in the same chromosome indicating that one is derived from the other; *I*—α_1, derived from γ_2; *J*—$\gamma_{2\text{-}3}$. The scale shown in *E* is for all figures.

ent studies not only add a number of new stages to those already known but also demonstrate a new type of series. These three series will be called the α-, β- and γ-series. Stages will be designated by the serial symbols with subnumerals which indicate the positions of the stages in the series; for example, the first stage of the α-series is designated by α_1 and the second stage of the β-series by β_2.

Since nearly always more than one stage appears on the same slide, the sequence in each series can be determined only from frequency-changes of the stages as the time of treatment is increased. The following case will explain the principle: With a 50% solution about 97% of the nuclei treated for one

minute are transformed to the a_1-stage while about 1% of the nuclei remain in the A-stage. Treatment for five minutes with the same solution produces the a_1-stage in 0.1% and the a_{2a}-stage in about 97% of the nuclei. After treatment for thirty minutes these stages disappear and the a_3-stage appears in 85% of the nuclei, most of the remaining nuclei being in a_6-stage. A further treatment for two hours produces the a_4-stage in 100%, and the still longer treatment (five hours or more) completely transforms a_4 to a_5. The order derived from the frequencies of the stages in the a-series produced by 50% mixtures is A, a_1, a_2, a_3, a_4 and a_5. Whether a_4 is derived entirely from a_3 or also from a_6 is not possible to determine from the above figures. Deficiencies in this method may be corrected by another method. This supplementary method depends on the fact that if the stages in question appear in different parts of the same chromosome at the same time, one of them may be considered to come from the other. In the particular case of a_4 and a_6, these stages have never been found together in the same chromosome. Therefore, it is considered that a_4 is derived entirely from a_3 and not from a_6.

The procedure of the first method is as follows: Glands are treated with each concentration for varying lengths of time and smeared with acetocarmine. Nuclei of every stage found in each slide are counted and the percentage of each is determined. The data are summarized in Table I. This table is so constructed that the stages of all series are shown in proper order determined according to the principle explained above. The table needs no detailed explanation except for the following: 1. In the case of the 10% solution a_{2b} takes the place of a_{2a}. This point will be explained in detail later. 2. Absence of the a_3-stage in the case of the 50% solution seems to indicate that the γ_2-stage is transformed to a_3 rather than to γ_3. 3. In the case of the 30% solution γ_3 can not possibly come from γ_2 alone, for γ_3 has a much higher frequency of occurrence (43.2%) than γ_2

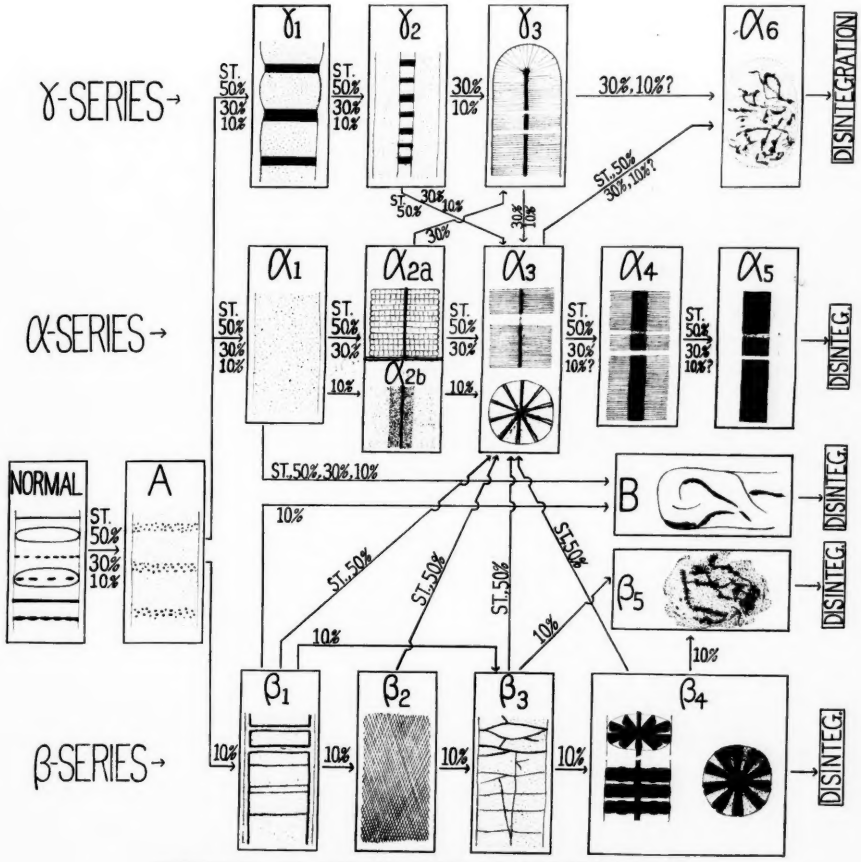
TABLE I. The stages of three series of transformation produced by 50%, 30% and 10% dilutions of the standard mixture are arranged roughly in the order of sequence determined from the frequencies of the stages, which are indicated by both the actual numbers of nuclei and the percentages. The order of the stages in each series varies slightly in different dilutions of the reagent (compare this table with Figure 4 for detail). * signifies all the observed chromosomes are transformed; M and L denote respectively more and less than about one-half of the observed nuclei are transformed; and + means that the stage was found in slides other than these which were used for the counting of the nuclei. For details see text.

Conc.	Time of Treatment	No. and % of Nucl.	Stages																				Total
			Normal	α-series: A	α_1	α_{2a}	α_{2b}	α_3	α_4	α_5	α_6	β_1	β_2	β_3	β_4	β_5	γ_1	γ_2	γ_3	B	
50%	15 sec.	No.		314																			314
		%		100																			
	1 m.	No.		7	650	9											6						672
		%		1.0	96.7	1.3											0.9						
	5 m.	No.			3	731											15	6		3			756
		%			0.1	96.7											2.0	0.8		0.4			
	10 m.	No.				703		51			1						5	20					780
		%				90.0		6.5			0.1						0.6	2.6					
	30 m.	No.						673			113							1		6			793
		%						84.6			14.2							0.1		0.8			
	2 hrs.	No.							*														
		%							100														
	3.5 hrs.	No.								*													
		%								100													
30%	15 sec.	No.		243	6												+						249
		%		97.2	2.8																		
	1 m.	No.		2	218	3											+						223
		%		0.9	97.8	1.4																	
	10 m.	No.			58	530		37			+						8	9					642
		%			9.1	82.7		5.8									1.2	1.4					
	20 m.	No.			+	+		169			+							2	130				301
		%						56.1										0.7	43.2				
	40 m.	No.						73			512								111		14		710
		%						10.3			72.0								15.6		1.9		
	4 hrs.	No.							M	L											+		
		%																					
	6 hrs.	No.							L	M											+		
		%																					
10%	1 m.	No.	42	556													+						598
		%	7.1	92.9																			
	3 m.	No.	1	664	35							92					+						790
		%	0.3	84.0	4.4							11.3											
	5 m.	No.		336	1							382					2			+			721
		%		46.6	0.2							52.9					0.2						
	10 m.	No.		12		+	+					220	169				1	+	+	82			497
		%		3.0								46.3	34.0				0.2			16.5			
	25 m.	No.					+					14	176	183	5					64			442
		%										3.2	39.8	41.4	1.1					14.5			
	40 m.	No.						4				6	1	771	90	62	2			14			949
		%						0.4				0.4	0.1	81.2	9.5	6.6	0.2			1.4			
	60 m.	No.												8	539	73							620
		%												1.3	86.9	11.8							
	1.5 hr.	No.												3	618	469			+	+			890
		%												0.4	69.5	52.1							

BETA-SERIES STAGES

Figure 3

Photomicrographs of various stages of the beta-series. *A*—β_1; *B*—β_2; *C*—β_2 under much higher magnification than *B*; *D*—β_3 (arrow points to the part where β_4 structure begins to appear); E_1, β_4 (the spiral structure is shown where the arrow points); E_2, the spiral structure of E_1 is shown under a much higher magnification. *F*, *G* and *H*, the successive stages of β_5-chromosomes. Scales are all 10μ.



SEQUENCE OF CHROMOSOME TRANSFORMATIONS

Figure 4

The essential structures and sequences of the stages of three transformation series produced by various concentrations of urea-alkali mixture are shown. The sequences are indicated by the arrows and the concentrations of the reagent by st. ("standard mixture") and percentages which are written above and below the arrows. For details see text.

(1.4%). Therefore γ_3 is considered to come mostly from a_2 whose frequency (82.7%) is much higher than that of γ_3.

4. By means of the supplementary method the *B*-stage has been found to follow *A*, a_1, or β_1, and to disappear without undergoing further transformation.

The three series of transformation explained above are summarized in Figure 4. It should be noted in this diagram that there are a number of minor variations in these major series of transformations. Some of these variations are already explained above and others can be readily understood from Table I.

Description of the Stages

The slides used for studies on the structure of the stages are prepared with acetocarmine unless otherwise stated. The Feulgen-Rosenbeck test is applied to all stages to determine the distribution of the nucleic acids with the result that the parts of the chromosomes which take

ALPHA AND BETA STRUCTURES

Figure 5

Photomicrographs of various stages of α- and β-series and of various structures produced by acid-alcohol mixture. *A1* and *A2*, optical cross-sections of coils of β_4 (*A2* is under much higher magnification than *A1*). *B*—Side view of a stretched coil of β_4. Note two pairs of chromonemata and the paired bulbs attached to the chromonemata. *C*—Side view of a β_4-chromosome showing where arrow points that the coils are not interlocked. *D*—The terminal bulbs (arrow) are shown to be larger in size than the others (haematoxylin stain). *E*—Free ends of *2L* and *X* including *In(X)d1-49* (note expansion of terminal coils, the heterochromatic regions, "a", "b", "c" and "d", in *X* and the stretched condition of the chromonemata in the heterochromatin "a"). *F*—β_4-chromosome treated with acid-alcohol mixture (note that the terminal set of bulbs is not dissolved). *G*—an α_3-chromosome treated with acid-alcohol mixture to show the existence of the membrane (2). *H*—A normal salivary gland chromosome treated with acid-alcohol mixture to show four chromonemata. *I*—α_4; *J*—α_5. Scales are all 5μ except *A2* which is 2.5μ.

up the carmine dye contain the nucleic acids. (It is assumed that the urea-alkali treatment does not produce to any significant amount a substance that gives a positive reaction to the Feulgen-Rosenbeck reagent from the substances other than the thymonucleic acids.) The structure of each stage observed in the aceto-carmine preparation would, therefore, indicate the distribution of the nucleic acids, and the consequent changing of the chromosome structure from stage to stage would show the way in which the nucleic acids migrate. Upon treatment with urea-alkali solution the nucleic acid in the discs first becomes diffuse, then migrates to the center of the chromosome and deposits on the chromonemata. Frequent reference to Figure 4 will help to clarify the following description.

The stages of the a-series. A: This stage is produced immediately after treatment with any dilution of the standard mixture and is characterized by the breaking up of all discs into discrete granules (Figure 2*A*). Some granules are scattered in the chromosomes in a chaotic fashion, the rest remaining in place. a_1: In this stage the granules are completely scattered in slightly swollen chromosomes leaving no trace of the original disc structure (Figure 1*A*). a_2: This stage shows a longitudinal chromatic string and finger-like chromatic bodies attached to the sides of the string along its entire length (Figure 2*B*). These finger-like bodies which are the masses of nucleic acid are cross-striated, the number of striations usually being six (see arrow in Figure 2*B*). The chromatic string is apparently the chromonemata incrusted with the nucleic acids. a_3: Upon further treatment the nucleic acid migrates to the chromonemata (see Kodani[13] for details), from the heterochromatic regions, not yet visible in the a_2-stage, and also from the finger-like bodies. Finally the euchromatic parts of the chromonemata become thicker and more chromatic while the finger-like bodies are reduced to thin hairs, the heterochromatic regions becoming entirely devoid of chromatin. This is the typical a_3-structure That the nucleic acid migrates away from the finger-like bodies is indicated by the actual presence of diffused nucleic acids in the spaces between the somewhat reduced finger-like bodies (see Figure 2*C* and the lower part of Figure 2*B*). The striated structure of the finger-like masses of nucleic acid sometimes remains in the hairs of the lampbrush chromosomes as a granular structure. Two chromonemata may be seen in each of the homologues where they are accidentally separated. (This is the first evidence for the four-strand structure.) Although a membrane around the chromosome is not visible in this or other stages of this series, its existence is demonstrated by the following experiment: Glands are treated with 50% mixture for thirty minutes so that nearly all chromosomes are transformed to the a_3-stage and then an acid-alcohol mixture (a mixture of equal amounts of glacial acetic acid and absolute alcohol diluted to 75% by addition of water) is applied for thirty minutes. Glands are then smeared with acetocarmine. In such preparations there may be found chromosomes parts of which remain in the lampbrush structure while the other parts are stretched and appear membranous (Figure 5*G*, 1 is the lampbrush part and 2 the membrane). The stretched lampbrush structure may be faintly visible inside the membrane. a_4: The chromonemata of the lampbrush chromosomes contract lengthwise and are incrusted with nucleic acid dissolved from parts of the hairs, so that in this stage the chromonemata are shorter and thicker while the hairs are distinctly shorter than those of the a_3-stage (Figure 5*I*). The cytoplasm is densely chromatic due to diffused nucleic acids. (The chromosomes are scattered in a mass of cytoplasm after complete destruction of the nuclear structure.) Diffusion of the nucleic acids into the cytoplasm is probably due to loss from the chromonemata of attachment surface for the nucleic acids on account of the enormous contraction. a_5: Dissolution of the nucleic acid of the hairs and deposition of some of the dissolved nucleic acid on the chromonemata continues until finally the hairs completely disappear in this stage (Figure 5*J*). The heterochromatic regions remain achro-

matic. The chromosomes of this stage seem to persist at least several hours, but dissolve and disappear on prolonged treatment. a_6: Following the a_3-stage various parts of the chromosomes, especially the hairs, dissolve so that a whole nucleus resembles a stage of the amphibian oöcyte (Figure 1*B*). Upon further treatment the chromosomes dissolve completely and finally disappear. Stage *B:* The chromosome of this stage is a partly collapsed membranous sac containing diffused chromatin (Figure 1*G*). It disappears after prolonged treatment without undergoing further transformation.

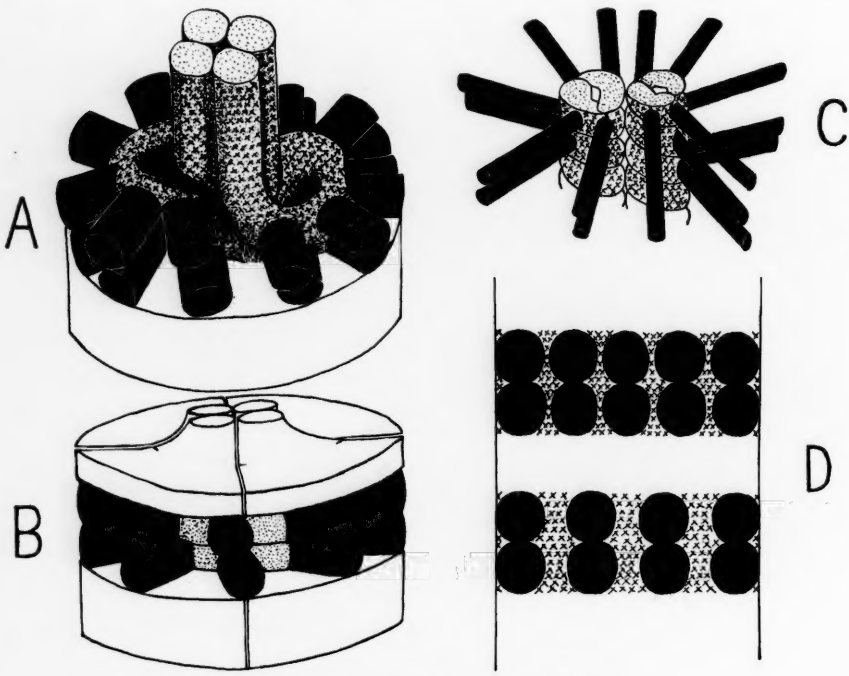
The process by which the lampbrush chromosomes are produced by a 10% mixture is slightly different from that described above. Treatment with 10% mixture produces first the *A*-stage, as in the case of the 50% and 30% mixtures, but following this stage chromonemata incrusted with nucleic acid are seen, through the densely diffused nucleic acid, along the center of the chromosome. This is the a_{2b}-stage Figure 2*D*). Upon further treatment the diffused nucleic acid is deposited upon hitherto invisible hairs and the whole chromosome is now in the a_3-stage (Figure 2*E*).

The stages of the β-series. β_1: The chromosome of this stage consists of a cylinder of nucleic acid whose edges appear as two chromatic lines, and a membrane which surrounds the chromosome (Figure 3*A*). The cylindrical structure of the aggregated nucleic acid is evidenced by the facts that a chromatic ring is visible in a lightly stained matrix in optical cross-section, and that four chromatic lines appear where the paired chromosomes are separated (Figure 7*B*), as would be expected if a chromatic cylinder splits into two cylinders. A membrane is clearly visible where the heterochromatic regions are overstretched (see 2 in Figure 7*A*). The cylinder of nucleic acid is interrupted along its length with a number of achromatic spaces; these have been proven to be the heterochromatic regions by the inversion method.[13] Sometimes in these achromatic spaces a few longitudinal chromatic threads may be observed. These threads are undoubtedly the chromonemata, and their number, to be specially noted, is never more than four (the second evidence for the four-strand structure). Furthermore, a number of faint, thin lines may be observed across the cylinder (1 in Figure 7 *A*). These seem to be remnants of the discs in the untreated chromosomes from which the nucleic acids are not yet completely diffused. The cylinder reduces its diameter, but not its length, on continued treatment and finally becomes a single longitudinal string. Hairs of nucleic acid appear at the same time so that the whole chromosome has a lampbrush appearance. This process may be taking place in Figure 7*D* where β_1 (1) and a_3 (2) are found in the same chromosome. Four chromonemata are sometimes clearly visible just before the lampbrush structure is formed. (Note the two twisting strings in one of the separated chromosomes (see arrows) in Figure 8 *A*. This is the third evidence for the four-strand structure). β_3: The nucleic acid does not always keep its cylindrical form while migrating to the center of the chromosome. In fact, some nucleic acid usually lags so that the cylinder gradually loses its straight edge (2 in Figure 7*C*) and finally disappears completely, a highly irregular net-like structure taking its place (see 3 in Figure 7*C* and Figure 7*G*. This is the β_3-stage. Figure 7*C* shows a part of a chromosome in which this process is shown by three successive stages indicated by 1, 2, and 3. At some parts of the β_3-chromosomes, dark crossbands and one or two longitudinal strings at the center of the chromosomes may be observed (see arrow, Figure 3*D*). These structures seem to become the coiled and stretched parts of the chromonemata in the next stage. β_4: The chromosome of this stage consists of partly coiled and partly stretched (Figure 7*F*) chromonemata, bulbs of nucleic acid which are attached to the coiled portions of the chromonemata, and a membrane. Figures 3*E*1 (arrow), 3*E*2, 7*H* and 7*I* show clearly the spiral structure of the chromonemata. The fact that the number of bulbs in a row, usually ten in lax chromosomes, may reduce to as few as two pairs in stretched chromosomes indicates also the spiral structure of the chromo-

nemata (Figure 8*F*). Arrangement of the chromonemata and the bulbs are shown in an overstretched part of the chromosome (Figures 5*B* and 7*J*). Note in these figures two pairs of chromonemata, each pair consisting of two strands which are winding around each other (the fourth evidence for the four-strand structure), and a number of paired bulbs which are attached to the side of the chromonemata. Coils of the sister chromatids do not interlock with those of the other chromatids as shown in Figure 5*C* (arrow) where two sets of coiled strands and their bulbs are slightly separated and run parallel to each other.

The number of pairs of the nucleic acid bulbs per coil was counted in a number of optical cross-sections and it was found that the number varies slightly from coil to coil, the most frequent number being ten (Figures 7*E*, 5*A*1 and *A*2). Two coils seem to be adjacent at some parts of the chromosome without being separated by a stretched part of chromonema. In the b-heterochromatic regions four chromonemata, fully stretched and bearing no nucleic acid bulbs, may be made visible by staining with haematoxylin (see heterochromatic region "a" in Figure 5*E*. This is the fifth evidence for the quadripartite structure). At the free ends of the chromosomes the bulbs are much larger in size and sometimes smaller in number, the coils usually being larger in diameter than in the other parts of the chromosomes (Figures 5*D* and *E*, arrows). The difference of the terminal set of bulbs from the others is also indicated by the fact that it is less readily dissolved by the acid-alcohol mixture than are the others. Note in Figure 5*F* that the bulbs are all dissolved except those of the terminal set indicated by an arrow. These observations seem to correlate with the idea of Darlington and Muller and of Haldane that the end genes donated as "telogenes" or ("telomeres" in terms of visible bodies) "constitute permanent chromosome structures distinguished from all other genes (or chromomeres) by their constant monopolar character."[18] The chromocenter may exist in the β_4-stage and appears as a network of beaded strings (1 in Figure 8*C*). In some cases four-beaded strings may be seen between the proximal end of the chromosome and the chromocenter (the sixth evidence for the four-strand structure). In instances where the chromocenter begins to undergo disintegration the bulbs of nucleic acid are found to fall apart (2 in Figure 8*C*). In such cases no threads are found to connect the bulbs. The poor organization, the low resistance to alkali and lack of mutation in this a-heterochromatin may be due to this lack of organized connecting threads (for details see Kodani[13]). It may be mentioned that when the chromocenter is completely absent the second arm of the IV-chromosome, shown to exist by Griffen and Stone[10] may be clearly observed (see the arrow in Figure 8*B*). The membrane is clearly visible in this stage (Figure 3, *E*1 and *E*2. β_5: Upon further treatment β_4 chromosomes undergo gradual dissolution and finally disappear (Figure 3*F*, *G* and *H*). β_5 is a stage where the chromosomes are only partly dissolved (Figure 3*G*). β_2: This is one of two cases in which the structure of the membrane is clearly observed, the other case being that of the β_4-chromosomes treated with trypsin, the details of which will be given later. The structure of this stage, as clearly shown by haematoxylin staining, is a network of fine fibers (Figure 3*B* and *C*). That the chromosomes at this stage are enormously swollen seems to indicate that in the untreated chromosomes the fibers are too close together to be seen as such and are made recognizable only when they are separated by swelling of the chromosomes. The network is cylindrical and contains a cylinder of nucleic acid (β_1), as clearly seen in some cases, indicating that this network is the membrane covering the chromosome. Furthermore, the fibers of this network contain practically no nucleic acid.

The stages of the γ*-series.* γ_1: Following the *A*-stage the chromosome contracts longitudinally so that some of the discs come very close together becoming thick and smooth (Figures 1*C* and 2*F*). γ_2: While lengthwise contraction continues the discs condense and some nucleic



INTERPRETATIONS OF STRUCTURE

Figure 6

Structures of the normal, β_4 and lampbrush chromosomes, as interpreted by the author, are shown diagrammatically in perspective (*A, B* and *C*) and side view (*D*). *A*—The straight and coiled parts of four chromonemata which are incrusted with nucleic acid (*X*) and the paired bulbs of the nucleic acid (black) of β_4-chromosomes are shown in the upper part of the diagram and the swollen condition of the straight part of the chromonemata in the normal chromosomes is shown below the coil. *B*—The spatial relation of the swollen and coiled parts of the chromonemata and the bulbs of nucleic acid (black) in the normal chromosomes is shown. The extrabulbar nucleic acid and the membrane are omitted. *C*—The arrangement of the paired hairs of nucleic acid and the tightly coiled chromonemata covered with nucleic acid (*X*) in the lampbrush stage is shown. *D*—The swollen interdiscal part of the chromonemata, the bulbs of nucleic acid (black) and the extrabulbar nucleic acid (*X*) in the normal chromosomes are shown in a side view. For details see text.

acid remains diffused in the chromosome. These features are shown in the γ_2-stage as illustrated at 1 in Figure 1*D* and in Figure 2*G*. The membrane is visible. A continued contraction of the chromosome and a simultaneous condensation of the discs finally produce a solid chromatic string along the center of the chromosome. Fine and usually granular hairs appear along the entire length of the chromosome as the chromatic string is formed. This is a typical lampbrush chromosome. The formation of the lampbrush structure from γ_2 is shown by the fact that γ_2 and α_3 structures are sometimes found together in the same chromosome (1 and 2 in Figure 1*D* and Figure 2*H*). $\gamma_{2\text{-}3}$: The structure of this stage is essentially that of γ_2 excepting that a distinct membrane is visible (Figures 1*F* and 2*J*). The granulated and ill-defined hairs may be visible. Condensation of the discs and the shortening of the whole chromosome continue and finally a typical lampbrush chromosome covered with a membrane is formed

(Figure 1*E*). The chromocenter is absent and the heterochromatic regions appear achromatic.

From the above description of various stages there is clear evidence that three different types of transformation are produced by the variation in speed and mode of migration of the nucleic acids from the discs to the center of the chromosome. A very rapid migration following attainment of complete diffuseness constitutes the α-series, a slow and irregular migration starting in the form of a cylinder following nearly complete diffuseness produces the β-series, and a relatively rapid migration without ever obtaining the diffuse condition gives rise tc the γ-series. The essential points presented in this section and the last sections are summarized in Figure 4).

Comparison of Normal and β_4-Chromosomes

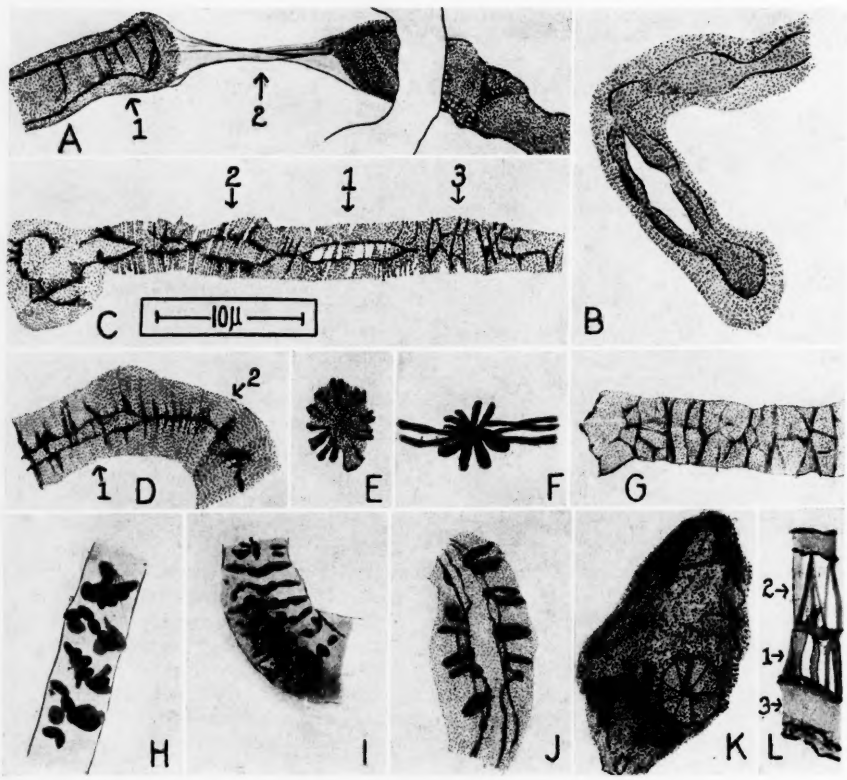
The lengthwise contraction of the chromosomes is readily visible in the γ-series, as we have just seen. In an attempt to find out whether or not a similar contraction occurs in the α- and β-series, the average lengths of the normal, α_3-, α_6- and various β-chromosomes were measured with the following results (all measurements were taken from lax chromosomes) ; Normal 3R, 70-100μ; 3R of α_3, ca. 45μ; α_6, ca. 13μ; 3R of β_4 and other β-chromosomes except β_5, ca. 90μ. These figures indicate clearly that a considerable contraction occurs in the α-series so that the chromosomes are reduced to about one-half of the original length at the lampbrush stage and to about one-seventh at the α_6-stage. In the β-series no appreciable contraction occurs.

If the coils of the β_4-stage were formed by treated straight chromonemata, the length of the β_4-chromosome should be considerably shorter than that of the untreated chromosome, provided the chromonemata do not elongate while they coil. The total length of a chromosome may be estimated by counting the number of the bulbs per coil and the distance between two bulbs (Figure 5*B*). The chromonemata must elongate enormously in order to attain the total length of all coils in a chromosome. Since it seems highly improbable that such an elongation occurs during treatment, the fact that the length of the β-chromosome is exactly the same as that of the untreated chromosome seems to indicate that the coils are already present in the normal chromosome.

If the coils correspond to the discs of the normal chromosome, the number of coils per chromosome should match the number of discs of the same chromosome. In a certain short section of a chromosome the number of coils was counted and compared with the number of discs in the same section of an untreated chromosome. The section proximal to the left breakage point of *In* (2R) *Cy* contains approximately 10 coils and the same section of the normal chromosomes usually shows about 10 discs. In the end section of the X-chromosome distal to the left breakage point of the *dl*-49 inversion the numbers of discs and coils were also found to match, if the discs of the b-heterochromatic regions are discounted. Since in b-heterochromatic regions the chromonemata are not coiled and the nucleic acid bulbs are lacking in the β_4-stage, exclusion of discs of those regions in the counting is necessary. The section proximal to the right breakage point of *In*(3L)*P* contains likewise the same number of discs and coils, provided the discs of the heterochromatic regions are ignored. These results seem sufficient to indicate that the number of discs in a chromosome is equal to the number of coils of the same chromosome, which in turn would seem to indicate that the discs and coils are structurally related.

Trypsin Treatment

If the stretched portion of the β_4-chromosome corresponds to the interdiscal region of the normal chromosome one would expect the stretched portion to be more quickly digested by trypsin than the coils, for it has been found by Caspersson[7] and by Mazia and Jaeger[17] that the interdiscal regions are less resistant to trypsin than are the discs in the normal chromosomes. In an attempt to test this the following experi-



DETAILS OF TREATED CHROMOSOMES

Figure 7

Camera-lucida drawings of various stages of β-series and other structures. *A*—β_1 showing cross-bands in the nucleic acid cylinder (1) and a membrane where the heterochromatic part is stretched (2). *B*—β_1 showing the appearance of four chromatic lines where the cylinder of nucleic acids splits. *C*—A part of a chromosome showing three successive stages, $\beta_1(1)$, an intermediate stage between β_1 and $\beta_3(2)$, and $\beta_3(3)$. *D*—A part of a chromosome showing two successive stages, $\beta_1(1)$ and $\alpha_3(2)$. *E*—Optical cross-section of a coil of β_4. *F*—Perspective view of a coiled part and stretched part of chromonema in β_4. *G*—β_3. *H* and *I*—Side view of a β_4-chromosome showing spiral arrangement of bulbs. *J*—Drawing of Figure 5*B*. *K*—Cross-section of a nucleus of α_3-stage showing section of one lampbrush chromosome (note some hairs in pair). *L*—A normal salivary gland chromosome treated with acid-alcohol mixture showing the cylindrical form of the chromonemata (1) and splitting of some cylinders where they are more stretched (2). The scale in *C* is the same for all figures.

ments were carried out: Glands were treated with 10% mixture for 90 minutes in order that most of the chromosomes would be transformed to the β_4-stage, and then were washed thoroughly with trypsin solution prepared according to Mazia and Jaeger. Glands were then incubated with the same trypsin solution at 37°C. After incubation for certain lengths of time the glands were treated with the Feulgen-Rosenbeck reagent to determine the distribution of the nucleic acids, and smeared. The Feulgen-negative chromosomes were then stained with Delafield's haematoxylin for about 12 hours. The controls were run in exactly

the same way except that boiled trypsin was used. While the chromosomes of the controls remained in exactly the same condition as the β_4-chromosomes, those treated with trypsin showed an effect within 90 minutes. The treated chromosomes were completely Feulgen-negative, and after staining with haematoxylin a coarse, fibrous network became visible (Figure 8*D*). Since this network was cylindrical and resembled closely the β_2-structure, it was considered to be the membrane of the chromosome. No structures that may have been the chromonemata were observed. Shorter times of treatment did not give any evidence for the lower resistance of the stretched part of the chromonemata to the trypsin solution than the coiled part. It may be mentioned, although it cannot be adequately explained, that the fibers of the network remained undigested for at least 24 hours and that the same trypsin solution required a longer time to digest the normal chromosomes than it did the β_4- chromosomes.

Nuclease Treatment

Frolova[9] treated the fixed and stretched salivary gland chromosomes of *Chironomus* with an extract of beef spleen (assumed to contain various nucleases) and found that the cross-striations remain and become stainable with acid stains after the nucleic acids were removed. Frolova's experiment has been repeated and confirmed in the following way: a ground beef spleen was soaked in a buffer solution (pH 7.1) of Na_2HPO_4 and K_2HPO_4 prepared according to Sőrenson and then filtered and centrifuged. The extract was applied to the smeared salivary gland chromosomes for 33 hours at 37°C. The boiled extract was used for control. The treated chromosomes were then tested for nucleic acid by Feulgen's reagent. While the control gave distinctly positive Feulgen reaction in the discs, the others were entirely negative. The latter were then first observed in glycerin jelly and later stained with light-green. It was found that after the nucleic acid was removed by nucleases the discs were distinctly visible in glycerin jelly and were stainable with light-green (Figure 8*E*). These results seem to indicate that some skeleton structure other than the nucleic acid exists in the discs of the normal chromosomes. If the discs of the untreated chromosomes consist of the coils of the chromonemata, the bulbs consisting of nucleic acids, the cross-striations remaining after removal of the nucleic acid indicate the presence in the bulbs of some kind of substance other than the nucleic acid. The lampbrush and β_4-chromosomes were also treated with the same extract under the same conditions. After the nucleic acid was completely digested, in the lampbrush chromosomes the central string remained while the hairs disappeared and in the β_4-chromosomes the coils and the other parts excepting the nucleic acid bulbs remained intact.

The above facts indicate the presence in the discs of the untreated chromosomes of some kind of "skeletal structure" which is resistant to nucleases, and the absence of this "skeleton" in the treated chromosomes due to its destruction by the urea-alkali solution. Whether this "skeleton" is a part of the bulbs or is in between the bulbs cannot be decided from the results of the above experiments. The author and another member of this laboratory have tried without success, by various methods, including those used in protozoology, to find this structure in the normal salivary gland chromosomes of *Drosophila melanogaster*. Perhaps this structure could be seen in *Chironomus* where the chromosomes are larger.

The evidence presented above seems to provide a sufficient basis to consider that the discs of the untreated chromosomes correspond to the coils of the chromonemata of the β_4-chromosomes. The generally accepted idea is that the salivary gland chromosomes represent a bundle of many chromonemata and that the individual discs represent the ultimate chromomeres (see Painter,[19] Koltzoff[15] and Buck[3] for detailed discussion). The foregoing experiments make it clear that the discs are not the ultimate chromomeres but consist of the coiled chromonemata and bulbs of nucleic acid attached to the sides of the coils.

That is, the discs are composed of about five ultimate chromomeres in a single chromosome, i.e., a half of a salivary gland chromosome, if the bulbs are actually the ultimate chromomeres. This does not necessarily mean that these ultimate chromomeres are the same as the chromomeres in leptotene chromosomes. The latter are probably combinations of many chromomeres.

On the basis of this consideration the enormous increase in diameter of the salivary gland chromosomes during development could be explained in either of the following two ways: 1. After pairing of the completely stretched chromonemata the coils of the chromonemata expand probably by means of molecular unfolding, or the amount of nucleic acid increases, or both occur together. 2. Prior to pairing the coils are stretched out and after pairing the coils are gradually reformed. The diameter of the chromosome would naturally increase as the recoiling proceeds. The first explanation seems to be supported by the observation of Painter[19] in *Simulium* and of Buck[3] in *Sciara* that after synapsis the paired chromomeres gradually enlarge without any visible division until they finally form the definitive discs. The second explanation seems to be supported by Alverdes's[1] claim in *Chironomus* that the synapsed chromonemata form coils during development which later break into separate coils and finally become the discs. There is no evidence at present that either of the above two processes is common to all cases or that both processes occur in different organisms. It may be mentioned here that on more or less substantial grounds Heitz,[11] Kaufmann[12] and Sinoto and Yuasa[22] assumed the presence of coiling in the salivary gland chromosomes.

Several explanations for the enormous elongation during development of the giant chromosomes have been suggested. As shown above, an a_6-chromosome (which is of course one arm of the chromosome) is about 13 μ. One arm of the leptotene chromosome is approximately 20 μ in length. The a_6-chromosome is, therefore, much shorter than the leptotene chromosome and hence it may be considered to be closer to the metaphase condition. A prolonged treatment of the a_6-chromosomes did not reduce the length to that of the metaphase chromosomes which is only a few micra. This is presumably due to lack of formation of major coils, and 13 μ seems to be about the limit of molecular folding. It is not difficult to conceive on the basis of these considerations that the increase in length of the developing salivary gland chromosomes is due to simple molecular unfolding especially in the interdiscal portion of the chromonemata.

In the normal salivary gland chromosomes some discs appear in usual acetocarmine preparations to consist of a number of chromatic granules. Some investigators have estimated the number of strands from the number of these granules assuming that each granule represents a homologous chromomere of a bundle of chromonemata. According to the present results regarding the structure of the discs, these granules are in some way related to the bulbs, if they are not actually the bulbs, and therefore to the real ultimate chromomeres of only four chromonemata. Hence, any estimate of the number of chromonemata from the number of granules is based on an erroneous assumption regarding the number of chromonemata and the structure of the discs.

Interdiscal Regions in Treated and Untreated Chromosomes

In some cases such as *Chironomus* and *Simulium*, longitudinal threads are said to be visible in the interdiscal regions. No such threads are observed in *Drosophila melanogaster* in usual acetocarmine smear preparations. But when the chromosomes are dehydrated and over-stretched similar types of threads do appear. These threads can be made visible by the following procedure: Glands are treated with the acid-alcohol mixture for thirty minutes and smeared. The chromosomes are then stained with haematoxylin according to the method described above. In such preparations longitudinal threads appear in most of the interdiscal spaces. The number of threads is most frequently four or less

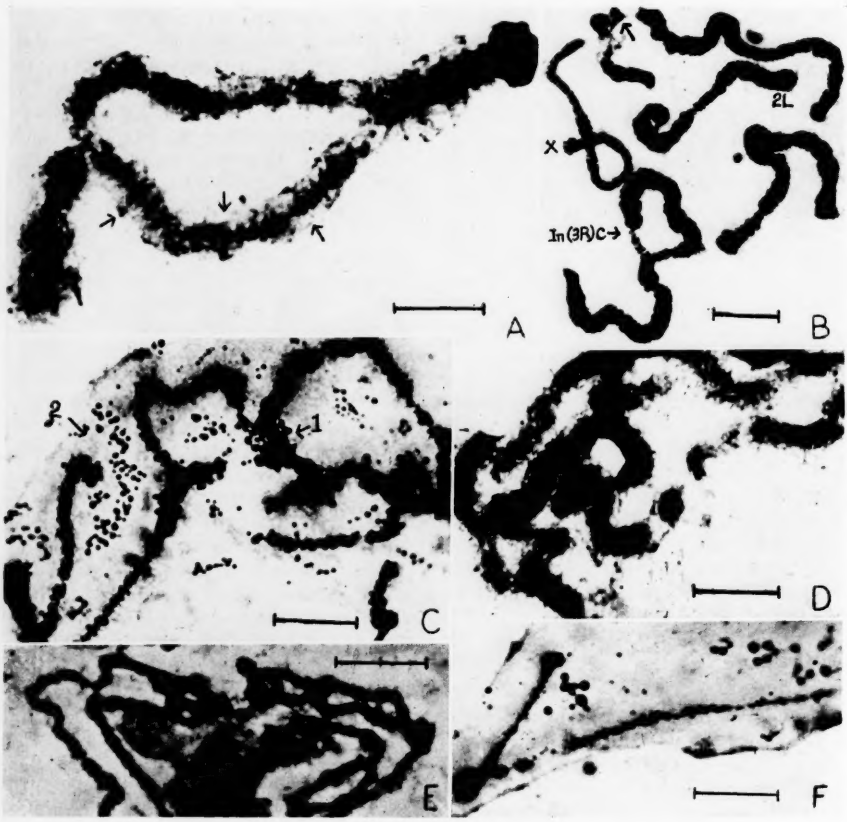
(Figure 5*H*) and they sometimes appear distinctly cylindrical in shape as shown at 1 in Figure 7*L*. In a space such as at 3 in the same figure where there is but very little stretching, four chromonemata are swollen and occupy the whole space. This is undoubtedly the condition of the chromonemata in the interdiscal regions of the untreated chromosomes. In over-stretched spaces such as the one shown at 2 in Figure 7*L*, the cylinders of the chromonemata are often split into smaller cylinders. This is undoubtedly a highly abnormal condition and the split cylinders of chromonemata can no longer be regarded as the true chromonemata: they are merely the groups of the protein micelles which as a whole constitute a single true chromonema. The fact that the observation by Painter[19] in *Simulium* and by Bauer[2] in *Chironomus* was made in stretched chromosomes suggests that the many threads which these investigators observed are an artifact of a similar nature and do not represent the individual chromonemata.

Nucleic Acid in Normal and Treated Chromosomes

The discs of normal salivary gland chromosomes appear either solid or granular in the usual acetocarmine smear preparation. Koller[14] showed that the solid discs appear granular under conditions of fixation which prevent swelling of the chromatin. Marshak[16] observed that in butylcarmine smear preparations the salivary gland chromosomes swell and the solid discs break up into granules. A mixture of acetocarmine and alcohol in a certain proportion produces a similar effect (details will be given in a future paper). There seems to be no doubt that all the discs consist fundamentally of a number of "granules" of thymonucleic acid. The solid appearance of some discs may be due to swelling of the granules as Koller suggested or to the presence of nucleic acid in the space between the granules. During treatment with urea-alkali mixture some nucleic acid migrates to the chromonemata while the rest reappears, after becoming diffuse, upon the hairs (α-series) or upon the bulbs (β-series). The nucleic acid which forms the hairs or the bulbs is considered to be the one which constitutes the granules in the untreated chromosomes, and the one which migrates and deposits on the chromonemata is considered to fill partly or completely the spaces between the granules. In Figure 6*D* the relation of these granular and extragranular nucleic acids is shown in a side view of an untreated chromosome. In Figure 6*A* (upper part) is shown the location of the extra granular nucleic acid on the straight as well as on the coiled parts of the chromonemata of the β_4-stage and the granular nucleic acid now reorganized into bulbs attached to the coiled portion of the chromonemata.

The foregoing interpretation suggests that the hairs of the lampbrush stage correspond to the bulbs of the β_4-stage. This suggestion is substantiated by the following facts: 1. Like the bulbs of the β_4-stage, the hairs of the lampbrush stage are in pairs as shown in the cross-section of an α_3-chromosome in Figure 7*K*. The same paired condition of the hairs has been observed also in optical cross-sections. 2. The β_4-chromosome can be transformed to the α_3-type by treatment with either a standard or 50% mixture. The bulbs of β_4 simply reduce in size as the result of dissolution and migration of some of their nucleic acid molecules to the chromonemata (see Figure 6*C*).

The other stages of the β-series with the exception of β_5 could also be transformed to α_3, if these stages were treated with the standard or 50% mixture (see Figure 4). As shown in Figure 4 all series of transformation lead irreversibly to the α_5-stage unless they end in *B*, α_6 or α_5 (which are relatively unstable) indicating that the α_5-stage is the most stable stage under the present experimental conditions. In case of the β-series, transformation ceases at the β_4-stage unless mixture of higher concentration than 10% is applied, because 10% mixture is too weak to dissolve the nucleic acid of the bulbs. When either the standard or 50% mixture is applied to the β_4-stage some of the nucleic acid of the bulbs is dissolved and migrates to the chromonemata thus giving rise to



BETA-SERIES DETAILS

Figure 8

Photomicrographs of various stages of the β-series and other structures. *A*—An intermediate stage between β_1 and α_3 showing two chromonemata which are twisted around each other in one of the separated chromosomes (arrows). *B*—A complete set of chromosomes in the β_4-stage showing particularly the second arm of IV (arrow) at the right of the first arm (a large spherical body). *C*—A nucleus in the β_4-stage showing partial disintegration of the chromocenter (note network structure of the undissolved part at 1 and disintegrated part at 2). *D*—β_4-chromosomes treated with trypsin and stained with haematoxylin and showing network structure. *E*—The normal salivary gland chromosomes treated with nucleases and stained with light-green. Note the cross-striations. *F*—An extremely stretched part of a β_4-chromosome showing the stretched condition of the coils as indicated by reduced number of bulbs per coil. All scales are 10μ.

a lampbrush chromosome which in turn will change to α_4 and subsequently to α_6 upon continued treatment.

When the β_4-chromosome transforms to the α_3-type, a very noticeable contraction occurs between the coils, that is, in the regions which are considered to correspond to the interdiscal spaces of the untreated chromosome, as shown by the shorter distance between groups of hairs of the α_3-stage than between the groups of bulbs of the β_4-stage. Contraction seems also to occur in the coils, because the diameter of the chromonemata in the

a_3-chromosome appears much smaller than that of the coils of the β_4-chromosome (compare Figure 5*E* and 7*K*). Contraction of the same parts of the chromonemata to a similar extent is considered to occur in both the a- and γ-series. This contraction of the chromonemata is not due to formation of extra coils but is due presumably to molecular folding. Possibility of molecular folding was demonstrated by Buck,[4] who by micromanipulation found that the interdiscal regions of the untreated chromosomes can resume their original lengths after being stretched as much as 300%.

General Discussion and Conclusion

Most of the discussion has already been made along with the description of the structures. Some points of general importance need to be considered now.

Koltzoff[15] found that the lateral loops attached to the chromomeres of the lampbrush chromosomes of *Triton* and chick are negative to Feulgen's nucleal stain. This absence of nucleic acid distinguishes the lateral loops from the hairs of the lampbrush chromosomes transformed from the normal salivary gland chromosomes, although these two structures are very similar in shape (excepting the loop formation in the former which is not the case in the latter) and relative arrangement to the axial strings as well as in the high solubility to hydroxyl ions (the lateral loops in *Triton* were found by Duryee[8] to dissolve readily in hydroxyl ions of pH above 8.4). Koltzoff and Duryee interpret these loops as the product of genic activities whereas Painter[20] considers these as the reduplicated chromonemata. Whichever may be the origin of these loops they seem to be different from the hairs of the experimentally produced lampbrush chromosomes, which are considered to be the structural variants of the nucleic acid granules in the discs of the normal salivary gland chromosomes. In view of these differences it is questionable that the natural and experimentally produced lampbrush chromosomes are identical in structure.

In experimentally produced lampbrush chromosomes a part of the dissolved nucleic acid deposits on the chromonemata while the rest diffuses into the cytoplasm ($a_3 \rightarrow a_6$). This seems to be due to the formation of a force of attraction, whatever it may be chemically, in the chromonemata by the action of hydroxyl ions, which causes the freely movable nucleic acid to migrate and attach to the chromonemata.

NaOH of one molar concentration has a rather low tendency to render the chromonemata visible as chromatic strings; that is, it does often produce the β-series of transformation where it takes as long as about thirty minutes for the chromonemata to become visible (see Table 1) and even when it produces the a-series, it often takes several minutes and sometimes even longer before the chromonemata show up. This low tendency seems to be due to a relative weakness of hydroxyl ions to split off the nucleic acid from the chromonemata, because when a proper amount of substance which is capable of easily dissolving the nucleic acid such as urea, KCN or acetamide is applied to the chromosomes simultaneous with NaOH, the chromonemata show up always and very rapidly, that is, the transformation is completely shifted to the a-type. As it was shown in a previous paper,[6] urea (and also KCN and acetamide), when used alone, carries the transformation only as far as to a_1-stage, that is, they diffuse the nucleic acid but do not cause it to deposit on the chromonemata. This seems to be due to inability of these substances, due to low basicity, to produce the force of attraction in the chromonemata. Deposition of the nucleic acid occurs only when hydroxyl ions (pH above ca. 11) are present in the reagent, and the rate of deposition is positively correlated with the concentration of the ions. Thus, when the proportion of urea (saturated aqueous solution) and NaOH (*1N*) is 9:1 the a_1-stage persists as long as 8 minutes whereas when the proportion is 1:9 the deposition occurs in one minute. It is quite evident then that what goes on in the salivary gland chromosome during treatment with urea-alkali mixture is simply the splitting off of the nucleic acid from the chromomeres main-

ly by the action of urea and subsequent deposition of a part of this nucleic acid on the chromonemata to neutralize the force of attraction which is produced there by chemical attack of alkali. This process seems to occur in both the α- and β-series in exactly the same way except that in the latter series the rate of deposition of the nucleic acid on the chromonemata is very much lower than in the former. In the γ-series this process does not seem to occur as extensively as in the other series, for the nucleic acid remains nearly entirely in the discs while the chromonemata contract (the small amount of nucleic acid which is dissolved is deposited on the chromonemata at the end of the series).

A question as to the relation of the nucleic acid to the chromonemata may be considered here. As already shown in a previous section, after the nucleic acid is removed by nucleases, the discs, the central string and both the coiled and stretched part of the chromonemata remain intact in respectively the normal, lampbrush and β_4-chromosomes. In view of these facts it is considered that the nucleic acid does not take part in the construction of the chromonema in the untreated chromosomes but is affixed to the chromonemata in the form of bulbs.

The essential structures of the normal salivary gland chromosome, according to the results of my experiments, are: 1. there are only four chromonemata, as substantiated by seven different proofs. Two of these four chromonemata are coiled intimately about each other and in each disc form a loop extending laterally. The other two are also coiled about each other and in each disc form a loop laterally in the opposite direction (cf. Figure 6*A*). 2. The discs consist of these coiled chromonemata plus the attached bulbs of nucleic acid (cf. Figure 6*B*). 3. The interdiscal regions consist of the four chromonemata, each of which is swollen and occupies one-fourth of the region (cf. Figure 6*B*). 4. The bulbs of nucleic acid, corresponding to the real ultimate chromomeres, are attached to the coiled parts of the chromonemata in the discs equidistantly apart (cf. Figure 6*B*). 5. The solid appearance of the discs in the normal chromosomes is due either to the presence of chromatin between the bulbs of nucleic acid or to a swelling of the nucleic acid bulbs themselves. 6. The whole chromosome is surrounded by a membrane. It is not certain whether the membrane really exists before treatment or is produced by treatment; however, the observation of a distinct membrane in the normal chromosome when treated with nucleases is in favor of its existence in the normal chromosomes.

It should be specially pointed out here that some discs in the normal salivary gland chromosomes are larger than the others. This is due either to the presence of more than one coil or to the larger amount of nucleic acid attached to a coil. As was shown in the description of the β_4-stage, some of these large discs are composed of two coils but this does not necessarily mean that all the discs consist of more than one coil: some may be large on account of a large amount of chromatin. This point will be clarified in a future paper.

It may be pointed out here that Painter observed in the ontogeny of the salivary gland chromosomes of *Simulium* that two homologous chromonemata divide once into four strands but no further division is visible. Buck found the same situation in *Sciara*. It is very likely that the chromosomes in these cases are also quadruple in structure.

The results of the present investigation indicate that Painter's interpretation[21] of the effect of alkali on the salivary gland chromosomes is untenable and also that the morphological interpretation given in a previous paper[5] is no longer tenable, except for the tetrad structure and the homology of the discs and the hairs of the lampbrush chromosomes. The final solution was possible only after the β_4-chromosomes could be produced by an improved reagent.

Summary

1. The salivary glands of *Drosophila melanogaster* were treated with 50%, 30% and 10% solutions of urea-alkali mixture for varying lengths of time at room temperature. The various appear-

ances of the chromosomes after treatment are classifiable into three major series of transformations: α, β and γ which are described and analyzed in detail. These three types of transformation are shown to be due to different modes of migration of some of the nucleic acid from its peripheral position in the untreated chromosomes to the chromonemata which are located in the center of the chromosomes.

2. Several observations show decisively that the number of chromonemata is four.

3. The structure of the β_4-chromosomes is considered for a number of reasons to represent very closely the structure of the normal chromosome. From this and other facts learned in the study, the structure of the normal chromosome is described (see Conclusion for details).

4. The different appearance of the coil and its nucleic acid bulbs at the free ends of the β_4-chromosomes substantiates the "telomere" concept.

5. Experiments indicate that a "skeleton" exists in the discs of normal chromosomes which is resistant to nucleases but is destroyed by urea-alkali treatment.

6. The structure of the lampbrush chromosomes produced by urea-alkali treatment is compared with the structure of the natural lampbrush chromosomes of *Triton* and chick described by Koltzoff.

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WHAT'S IN A PLANT NAME?

EXCEPTING the few who, for professional reasons, specialize in aliases no one expects to find his friends known by different names in different places. Hardly more does he expect to find in some locality several friends with identical names. The endless confusion that would result were such a condition to exist staggers the imagination. Yet just this situation is found with respect to the names of plants and it is not restricted to the rare and little seen sorts. It is the plants universally used that acquire long lists of aliases. Equally bad is the fact that many plant products with the same common name have not a common origin. Take, for example, mahogany. Under present widely accepted terminology you may have three pieces of mahogany furniture, one made from the true mahogany tree of the West Indies, *Swietenia mahagoni;* one from the African tree, *Khaya senegalensis;* and the third from the Philippine tree, *Pareshorea malaanonan.* This does not exhaust the possibilities of mahogany but is enough to show the situation with respect to a single widely used wood.

Botanists have operated under an international code in devising and assigning scientific or Latin names to plants. Although this system is far from perfected it has established a workable degree of order among those whose professional interests are classificatory. Most plants of any utility have also acquired fancy, common, or trade names by which they are known to those who use, grow, or sell them. These names, actually much more widely current than the Latin names of the botanists, were assigned by whim without rules and regulations and usually with little rhyme and less reason. To bring order out of this chaos and confusion a group of indefatigable plantsmen began a little more than a quarter of a century ago to establish rules of nomenclature and to produce a list of standardized popular names of plants. The first edition of *Standardized Plant Names* was issued in 1923 under the editorship of Frederick Law Olmsted, Frederick V. Coville, and Harlan P. Kelsey for the American Joint Committee on Horticultural Nomenclature. Although not expected to bring about a revolution in plant naming it met with general approval and its code will, with time, achieve the desired order. That the first effort was accepted and appreciated is proven by the appearance of a second edition* which is before us today.

Expanded, improved, and brought up to date under the rules promulgated in the first edition this second edition is doubtless only the second generation of a long line of worthy successors. The new edition has 675 pages, including the glossary, in a three column format. Although the reviewer has not made an exhaustive check, it has been found by sampling to be adequately cross-indexed, which is an important consideration in a work of this nature. The editors credit the indexing to Miss Catherine E. Meikle of the Mount Pleasant Press.

The prospective purchaser needs to be assured that the list is complete and that it enjoys the approval of the professional plantsmen. The present volume contains, in addition to its regular listings, sixty-two special lists (in alphabetical position) such as aquarium plants, drug plants, fiber plants, lumber trade names, and a complete list of plant patents from 1 to 477, as complete as the editors with their collaborators could make it in the space available. It does not contain names of horticultural varieties of gladiolus or of iris — the latter having an official published list of the recognized 19,000 varieties.

A word should be said about the editors who, after all, have performed a herculean labor of love. Of those who served on Volume One only Harlan P. Kelsey survived to father the second edition. In this undertaking he was aided and abetted by William A. Dayton of the U. S. Forest Service. To these gentlemen all those interested in plants (and few indeed are not in some manner so interested) owe a real debt of gratitude. Without their drive the job simply would not have been done for this is one of those monumental tasks that every thoughtful person recognizes needs be done. While many are thus "called," few, indeed, are willing and able to devote their time, and particularly to exercise their patience, to bring such a work to so satisfactory a conclusion.

The editors believe the burden of future editions should be assumed by some of the governmental organizations whose work is with plants. This seems logical especially from the standpoint of underwriting the costs of printing and binding, thereby reducing the price and achieving perhaps a more widespread use. However, it is seriously questioned whether any single governmental organization could command the widespread cooperation of institutions and individuals won by the editors of this second edition.

The reviewer recommends early purchase as it may be far more than 19 years before the third edition makes its bow and in the meantime this second edition will stand without challenge as the definitive work in this field.

J. H. Kempton
U. S. Department of Agriculture

**Standardized Plant Names* edited by Harlan P. Kelsey and William A. Dayton. Pp. 675, $10.50, J. Horace McFarland Co., Harrisburg, Pa. 1941.

AUTO-SEXING IN THE DOMESTIC PIGEON

W. F. HOLLANDER*

EXTERNAL differences between male and female pigeons are slight and variable. Even breeders of considerable experience are often mistaken in separating the sexes, especially in the case of immature specimens, and they consider it practically impossible to sex squabs. It would seem therefore that some of the methods by which poultry breeders have succeeded in sexing baby chicks might be applied to advantage in the case of pigeons.

One method of sexing chicks which has been very successful is the sex-linked mating. With pigeons there are plentiful opportunities to use this method. Nearly every breed has common sex-linked color factors, so that an almost endless number of crosses within and between breeds permit sexing of the squabs by the age of two weeks. Nevertheless, the sex-linked mating has not become popular with pigeon breeders. One reason seems to be that the method is too technical to appeal to pigeon breeders; another, the fact that only a certain proportion of one's matings can be of this kind. In commercial squab production there is a third reason (although here the method has won a certain amount of favor): many sex-linked matings produce squabs with dark skin — a feature not detrimental to edibility but disliked in most markets.

A second method of sexing chicks is the "Japanese" or "look-see" method. By partial eversion of the chick's cloaca, an expert can recognize differences between male and female structure, as the male possesses a rudimentary copulatory organ. This method is not quite so sure as the sex-linked mating, but obviates the necessity of crossing and certain other difficulties.

An application of this method to pigeons was made by Iwata,[9] who claimed to be able to sex both old and young with ease. Unfortunately his report is limited to claims and drawings, with no substantiating data. A careful test with squabs from sex-linked matings has demonstrated to my satisfaction that Iwata's method is erroneous. Furthermore, as the male pigeon has not even a vestigial copulatory organ like that of the male fowl, a "look-see" method seems unlikely to be perfected.

There remains a third method of sexing chicks, which is now known as auto-sexing. This is a genetical method, involving a sex difference in appearance of the chicks, but it is unlike sex linkage. The inheritance is more like that of sex-limited characters. That is, in sex-linked crosses son is like mother, daughter like father, while with auto-sexing this "criss-cross" effect is absent — son is like sire, daughter like dam. And instead of being a one-generation phenomenon like sex-linkage, auto-sexing continues indefinitely without attention.

The elimination of technical complications makes auto-sexing a desirable method. The accuracy is often lower than with the preceding methods in the fowl,[10] but errors are seldom over 10 per cent.

With pigeons there have been occasional suggestions of sexual dimorphism, but until very recently auto-sexing seemed an impossible dream. It is the purpose of this paper to show the possibilities of the method.

Auto-sexing in General

The term "auto-sexing" was originated by poultry geneticists within the last decade. In the reports of Lamoreux[10] and previous workers it has been demonstrated that a sex-linked dominant factor for barred plumage coloration is the basis for auto-sexing varieties of chickens. The males are homozygous for the "Bar" factor, and the females also

*The data here reported are from a project under the writer's care at the Palmetto Pigeon Plant, Sumter, S. C.

have the factor, but as the females have only one sex chromosome they must be termed *hemizygous* rather than homozygous or heterozygous. The difference between homozygosity and hemizygosity is associated with a corresponding difference in coloration between male and female chicks. The heterozygous males are not distinguishable from the females. From the genetic facts it seems unlikely that sex hormones play any role in the dimorphism; in addition, the fact that the differences are quite apparent in infancy before the gonads become active leads to the same conclusion. Not all sex-limited differences in gallinaceous birds are dependent on hormones, as shown in experiments by Danforth.[1]

As there are several other known sex-linked factors in the chicken, it may be asked why "Bar" alone can be used in auto-sexing. This question may best be answered by considering the facts in the case of the fruit fly, *Drosophila*, where a similar situation exists. Of the numerous sex-linked mutants in *Drosophila*, very few show a dimorphism between the homozygous and hemizygous conditions. Those which do show dimorphism may be dominant (e.g., "hairy wing" and "beadex") or recessive (e.g., "eosin"). Incomplete dominance, which Lamoreux considers the most important feature of the "Bar" factor in fowls, appears to have nothing to do with the dimorphism in *Drosophila*; the sex-linked "Bar Eye" factor is incompletely dominant but not sexually dimorphic. An experimental analysis of the problem was undertaken by Muller, League, and Offermann,[11] using chromosome deficiencies and duplications. They concluded that dimorphism is simply a dosage effect, and to be expected, while the more common lack of dimorphism is apparently due to some unknown compensatory mechanism. The question with which this paragraph began cannot therefore be answered satisfactorily at this time.

A condition like auto-sexing has been known in certain breeds of geese for many years.[12] Unfortunately the genetic basis here has not been analyzed. Darwin[3] commented on the same sort of sexual color dimorphism in the wild Rock Goose, *Bernicla antarctica*, but whether the difference is apparent in the young of this or of other wild birds does not appear to have been discussed.

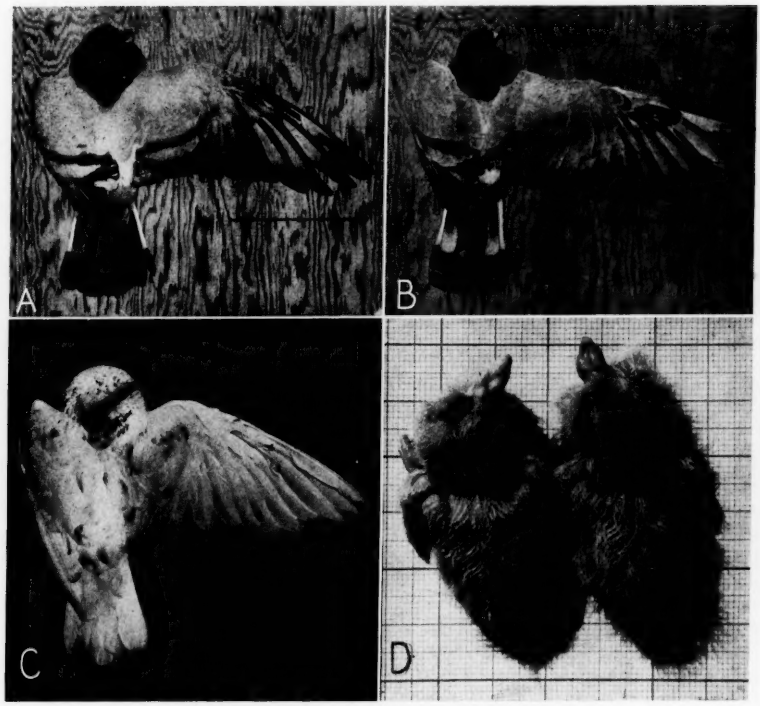
Sexual Color Dimorphism in Pigeons

Nearly 70 years ago Darwin mused on the possibility of creating a sex difference in color of pigeons. He concluded[2] that, provided the initial variation were limited to one sex, "there would not be the least difficulty in making a breed with the two sexes of a different color, as indeed has been effected with a Belgian breed in which the males alone are streaked with black" (p. 247).

In spite of Darwin's statement that this sexually dimorphic "Belgian breed" had been produced, nothing further is known of it. Probably it never got beyond the promising stage, according to our present knowledge of the condition "streaked with black." The mutant factor involved was almost undoubtedly the common "ash-red," a sex-linked dominant. Males heterozygous for "ash-red" and wild type ("blue" and black) generally show a number of scattered flecks and streaks of wild-type coloration in the plumage, while the "ash-red" female (hemizygous), shows few if any flecks, and even these differ from those of the heterozygous male, as they are brown in color.[8] To that extent there is a sexual dimorphism, but no pure "breed" could be established to maintain it because the *homozygous* males are indistinguishable from the females.

Two other common sex-linked factors in pigeons do not permit auto-sexing: "brown" or "chocolate", a recessive, allelic to "ash-red"; and "dilution", a recessive, situated at a considerable distance from the "ash-red" locus on the sex chromosome.

There are two remaining known sex-linked factors, "almond" and "faded", and with them auto-sexing is possible. Both are dominant to wild type, and appear to be alleles not only of one another but also of "ash-red" and "brown."[8]



SEX-DIFFERENCES DUE TO "FADED" GENE

Figure 9

A—Wild-type coloration; *B*—a "Faded" female; *C*—a homozygous "Faded" male; *D*—a pair of day-old squabs from an auto-sexing mating: note the shorter down and non-pigmented beak of the male (left).

Almond

The "almond" factor is found chiefly in Almond Tumblers and in Magnani Modenas, but also is found occasionally in other breeds. In young birds the coloration is very light — dirty whitish to buff — with scattered flecks and streaks of darker coloration, usually wild type. With age the flecking increases, sometimes practically excluding the original light color. The male generally shows these flecks more extensively than does the female, but not always.[5] The homozygous male is not included in the above comments, as it has never been adequately studied, but there is a good deal of evidence that it is *white*, with few obvious flecks. Breeders of almond-colored pigeons seldom mate like with like, so that the homozygote would be rarely observed. This unusual breeding practice is of some antiquity. Fulton[4] writing in 1874 says (p. 152): "Some fanciers we have known match up two good Almonds. . . . We will not affirm it is so in all cases, but we can state with confidence that when this is done, the result is very seldom at all satisfactory, the progeny being generally light-colored Agates or Splashes, or too often nearly all white." And again (p. 153): ". . . one thing above all others should be carefully avoided, and that is, breeding together two soft-colored Almonds, the

progeny being generally Mealy Chequers, Chequered Duns, or bull-eyed White Splashes."

The heterozygous nature of ordinary almond males is clearly indicated by the above quotations. Other evidence that the homozygous males are white is available in unpublished data obtained by Dr. H. W. Feldman. In breeding tests, no males of ordinary almond coloration were found to be homozygous, while matings of almond × almond generally produced some white offspring. Although further study is advisable, it appears that auto-sexing can be accomplished with the "almond" factor, and that breeders have long missed the opportunity because of their peculiar breeding rules.

The utility of the "almond" factor for auto-sexing may be hindered, however, in several ways. There is some indication that the eyes of the homozygous males are abnormal, at least in certain families. Fulton[4] describes individuals with black "bladder eyes," and similar specimens are being studied by R. E. Gilbert. These birds are blind or nearly so. Wriedt and Christie[13] also found defective eyes in an almond variety. These authors furthermore consider the "almond" factor deleterious to the vigor of squabs, especially in combination with the "dilution" factor. Both of these factors reduce the length of the nestling down, so that the squab is less well protected than normal, and the homozygous "almond" probably is even closer to nakedness.

Faded

The "faded" factor is the last of the known sex-linked factors, having been first reported by the author only about four years ago.[6] Little breeding information was available at that time. In 1940, Hollander and Cole[8] presented additional facts, and concluded that "faded" is allelic to "almond" and "ash-red." The phenotype of the "faded" female is indistinguishable from that of the male heterozygous for wild type, and is about what the name suggests: a general, though often not very conspicuous, fading of coloration in comparison with wild type. Flecks of wild-type coloration may occasionally occur in the plumage. No homozygous individuals had been produced for study before the spring of 1940.

At that time the only birds known to be of the "faded" type were in the University of Wisconsin laboratory. However, a few specimens of unrelated origin but apparently of the same type had been found and were being tested at the Palmetto Pigeon Plant in Sumter, S. C. They had been produced in matings of "self-white" Carneau males with blue-black Homer females. Identity with the previously known "faded" was soon shown, not only by phenotypic similarity but by the fact that it is dominant and sex-linked, and has given no crossing-over with "ash-red" or "brown", but abundant crossing-over with dilution.

Matings of "faded" individuals of the new stock *inter se* have consistently produced a novel coloration in a certain proportion of the offspring. Superficially the new type appears white, but closer inspection shows a slight general pigmentation, from a dusty gray to a yellowish or reddish tinging or tipping of the feathers, especially those of the neck. In addition there are usually scattered flecks and streaks of ordinary "faded" coloration, and in a few cases small patches of "faded" feathers. It was noted also that squabs which developed this coloration had shorter than normal nestling down, though not so short as with the "dilution" factor.

The novelty of this type, and the fact that it was produced in all matings of "faded" × "faded" indicated that it was the homozygote. Without exception these birds (about a dozen in number) were males, as the homozygote must be. Two of these males were outcrossed to non-"faded" females, and over twenty offspring resulted, all "faded."

The males of the new type were normal in fertility and vigor, and gave promise of being excellent material for founding an auto-sexing strain. Accordingly matings with "faded" females were made up and all healthy offspring raised to

maturity. The offspring were either like the father or the mother, as predicted. Twenty-five of them have been sexed definitely by breeding tests or by post-mortem observation, and without exception the "faded" individuals were females, while the whitish birds were males. In addition several squabs which died before plumage coloration had developed but which had pigmented beaks were all females.

Down length of the young squab has proved to be a very reliable sex indicator in such matings, the males having shorter down than the females (see illustration). Beak coloration was also an excellent indicator, at least for females. The presence of pigment in the beak classifies the individual as a female, no males having such pigmentation. However, non-pigmentation of the beak is not always the sign of a male, for white-spotting or piebaldness, if present in the stock, may also eliminate pigmentation. It should be mentioned that piebald young were frequently produced in some of the above "faded" × "faded" and also in some of the auto-sexing matings, but classification of the young was not prevented. Furthermore, two of the auto-sexing matings produced a few "self-white" squabs, which were classified correctly on the basis of down length. The segregation of the "self-white" condition was expected in view of the fact that the birds were only two or three generations removed from the "self-white" Carneau. This type of white is extremely common in pigeons; its inheritance is not yet clearly established, as it appears to be closely related to white-spotting or piebaldness, but there is no connection with sex. Piebaldness and "self-white," as well as other mutant color factors, seem best eliminated from an auto-sexing strain, to make sex distinction most obvious and clear-cut.

The iris coloration of the homozygous "faded" males deserves comment. The bright pigment is slow in appearing, and never becomes rich. The final appearance resembles somewhat the mutant "pearl," studied by Hollander and Owen[7] though the former is more dusky. Some of the males had practically no anterior iris pigment, but this probably was due to the presence of piebaldness and was not typical. By contrast, the iris of the female or heterozygous "faded" is usually yellow or orange, indistinguishable from that of the wild type.

The greater prevalence of flecking in the homozygous as compared with the heterozygous and hemizygous "faded" supports an argument made in the general study of flecking in birds by Hollander and Cole.[8] There it was suggested that flecking is due to somatic mutation, and that where the phenotype of the homozygote is distinct from that of the heterozygote, as in the case of the Andalusian fowl, the homozygote will show approximately twice as much flecking as the heterozygote. That is, there are twice as many mutable factors in the homozygous bird, and the flecking should be correspondingly increased.

Practical Applications

Exploitation of "almond" in auto-sexing will probably not prove worthwhile except for laboratory study because of the undesirable features accompanying the homozygous condition, as discussed above. On the other hand, "faded" seems to be the answer to the commercial squab producer's prayer. Not only is the sexing practically foolproof, but the squabs' skin color is light—never dark enough to be disqualified in the market.

At the present time the factor is being introduced into several breeds for commercial use; when the process has been completed these breeds may be used in a variety of cross-breeding programs to obtain F_1 vigor. It is planned not to use new breed names as poultry geneticists have done (e. g., "Cambar," "Legbar," "Ancobar," "Oklabar"), but to use the present breed name and the descriptive term "dual-colored," or "auto-sexing."

Summary

Auto-sexing is shown to be possible with two dominant color factors in the domestic pigeon. These are "almond"

and "faded." The latter appears to have the greater utility as sex distinction can be made at hatching on the basis of down length and beak color, and vigor is normal. The adult homozygous "faded" male is described.

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Science and Technology

It seems high time to break up this ancient tradition of intellectual royalty and substitute a group of the sciences based upon the more democratic conception of the division of labor. The two main functions of science are explanation and control or application. In such a grouping explanatory science must always have a place of central importance. But explanation for the sake of explanation, or explanation as mental exercise, or mental discipline, can hardly be considered moral in an age so beset by life-and-death problems as is our own. The pedagogy of such a pursuit is also open to serious criticism.

Explanatory science deals with cause and effect relations, and has as its aim the establishment of facts and laws. Applied science or technology, on the other hand, deals with problems of means and ends, and should aim at the production of values. Mr. Aldous Huxley thinks that it is a mistake to separate problems of scientific techniques from those of social values in professional training. Besides teaching young men to be mechanicians, for example, he thinks that we should teach them "to understand the ways in which machinery affects, has affected and is likely to affect, the lives of men and women." Certain it is that, in the absence of any feeling of responsibility in such matters, the more highly specialized a professionally trained person is, the more of a menace to society he can turn out to be.

Technology should assure responsibility for two somewhat distinct problems. In the first place it should seek to ascertain what sort of means will produce what sort of ends. This problem is as simple and as clear-cut, and as factual as are the problems of cause and effect with which explanatory science undertakes to deal, and the methods of inquiry called for in the case are not different from those employed in theoretical science. In the second place technology, or applied science, must, if it is to carry out its part of a joint undertaking, devise ways and means of determining which ends are good and which are bad. This is the crux of our problem. Granted that this is a field of inquiry from which by common consent science has for the most part in the past been barred, does this settle the question? It is not a new event in the history of science to explore hitherto unexplored territory.

Can the knowledge and the technical skills of our time be brought to bear upon the confusions that characterize human relationships everywhere? Upon the answer to this question depends the unsettled issue concerning man's ability to govern himself, for, in spite of our miracles of discovery and achievement we have been accused of living in a Stone Age sociology.—JOHN M. FLETCHER, *Scientific Monthly*, March, 1942.

ON THE BREEDING OF ARYANS

And Other Genetic Problems of War-time Germany

TAGE U. H. ELLINGER

DURING a visit to Germany in the winter of 1939-40, I had an opportunity to meet some of my fellow geneticists, who seemed to be working undisturbed by the campaign and the "mopping up" in Poland, and by the hectic preparations for the assaults on a great many peaceful countries such as Denmark, Norway, Holland, and Belgium. The following unpretentious notes, written for laymen, may perhaps interest some of their many American friends.

Quite a few of them were busy treating or rather mistreating the sex cells of animals and plants in order to produce new varieties. I was introduced to all kinds of extraordinary creatures produced in that way, mice without toes or with corkscrew tails, flies that violated the very definition of a fly by having four wings instead of two, funny-looking moths, and strange plants.

Radiation, especially with X-rays, is the principal means of producing such new kinds, or rather monsters, of animals and plants, and the wizard in this business was a Russian, Dr. Timofeeff-Ressovsky, who has found an asylum at the Kaiser Wilhelm Institute for Brain Research. An industrial concern has presented him with the enormous machines with which he radiates the minute sex cells of tiny little Drosophila flies.

Timofeeff is a fanatic and an enthusiast. I was really spellbound while he gave me a three-hour lecture on his work, incessantly gesticulating as he walked up and down the floor. The German staff of the Institute looked at this strange and temperamental Russian with amusement and sincere admiration. They even granted him a freedom of speech and opinion they would deny any other human being.

Genuine German thoroughness characterized Professor Nachtsheim's elaborate experiments on the heredity of disease. Since one can not very well make human patients mate and produce numerous babies to suit the analysis of a pathological problem, he had resorted to rabbits. These obliging and fertile animals suffer from a great many troubles like our own. It was a pathetic sight to look at the hundreds of incurables in the rabbit houses. But at that, our own institutions housing people afflicted with hereditary diseases are no less disconsolate.

When I went to see the famous old "Geheimrat" Fischer at the Kaiser Wilhelm Institute for Anthropology, an S.A. man in black uniform was present during the conversation. He was introduced as Dr. Abel, and the director afterwards asked him to show me around. The result was that we spent several days together.

Twins in the "New Order"

Twins have, of course, for a long time been a favorite material for the study of the relative importance of heredity and environment, of nature and nurture. It does, however, take a dictatorship to oblige some ten thousand pairs of twins, as well as triplets and even quadruplets, to report to a scientific institute at regular intervals for all kinds of recordings and tests.

I was particularly interested in their laboratory for the study of the inheritance of behavior and mental capacities. For this purpose, the twins were placed in two identical rooms, separated by a narrow corridor for the observer, who had a free view over both rooms through big windows in the walls. These, however, were fitted with that remarkable kind of glass through which you can see in one direction

only. From the other side, these windows looked like ordinary reflecting mirrors. This may serve as a warning that in Germany even an unbroken mirror may bring seven years' bad luck if it happens to conceal an observer who does not feel that one's behavior is up to proper Aryan standards.

If the observer wants a permanent record of the behavior of the twins, he can operate two concealed movie cameras with the lenses nicely camouflaged in the wall paper.

Racial Diagnosis

Dr. Abel's principal work was, however, in connection with the racial policy of the Nazi government.

In itself, the problem is a fairly simple one when it is first understood that the deliberate eradication of the Jewish element in Germany has nothing whatever to do with religious persecution. It is entirely a large-scale breeding project, with the purpose of eliminating from that nation the hereditary attributes of the Semitic race.

Whether this be desirable or not is a question that has nothing to do with science. It is a matter of policy and prejudice only. It is a problem similar to that Americans have solved to their own satisfaction with regard to their colored population. The story of the cruel ways in which life has been made unbearable for millions of unfortunate German Jews belongs exclusively in the shameful realm of human brutality. But when the problem arises as to how the breeding project may be carried out most effectively, after the politicians have decided upon its desirability, biological science can assist even the Nazis.

The first question that faced Dr. Abel was to find out exactly what are the hereditary peculiarities in which Jews and non-Jews, or "Aryans," as they are called, differ. It is a problem of exactly the same nature as if you were asked to record the exact hereditary differences between a bird dog and a hound. It has nothing whatever to do with your personal preference for one or the other.

It is a matter of common knowledge that anybody can immediately recognize many Jews by simply looking at them. In other words, the Jew has a number of characteristic bodily features not often combined in a non-Jew or "Aryan." In addition, he may display certain mental characteristics you would soon notice by personal association. Leaving these aside, it becomes a matter of keen but fairly simple analysis to determine exactly what these Jewish features are, expressed quantitatively in numbers, measurements, and weights.

The next thing is to find out the behavior of such of these characteristics as are inherited in later generations following a cross between a Jew and an Aryan. Seen from the standpoint of a pedigreed dog, we are all mongrels, and some of us show recognizable inherited characteristics contributed from one or more Jewish ancestors. This is a plain fact, and has nothing to do with relative superiority or inferiority.

An amazing amount of unbiased information has accumulated dealing, for instance, with such features as the position of the ears, the shape of the nostrils, etc. As a result, it is quite possible, by studying the bodily features of a person and his relatives, to state, with considerable likelihood of being right, whether this person has Jewish ancestors or is a straight descendant from old man Wotan.

If it be decided by the Nazi politicians that persons with Jewish ancestors shall be prevented from mating with those who have not such ancestors, science can undoubtedly assist them in carrying out a reasonably correct labeling of every doubtful individual. The rest remains in the cruel hands of the S.S., the S.A., and the Gestapo.

What I saw in Germany often made me wonder whether the subtle idea behind the treatment of the Jews might be to discourage them from giving birth to children doomed to a life of horrors. If that were accomplished, the Jewish problem would solve itself in a generation, but it would have been a great deal more merciful to kill the unfortunates outright.

"Aryanizing" the Ancestry

As things are run in Nazi Germany, it is obviously a matter almost of life and death whether you carry the label Aryan or Jew. Since the authorities, however, are interested in biological rather than in legal parentage, their policy opens a possible loophole for children of an Aryan woman married to a Jewish man. If it can be proved that her child is actually the result of illegitimate sexual intercourse between the mother and an Aryan man, such a child will be registered as an Aryan despite the race of his legal father. The most talked of story of this kind deals with a famous Air-Marshal and right-hand man of General Field-Marshal Goring, who at least legally was supposed to be a Jew.

It is perhaps human that a very large number of such unhappy mothers, who tremble for the fate of their children, make frantic efforts to prove to the satisfaction of the authorities that they have committed adultery. If they want to submit to such an investigation, they have to apply to the pedigree office ("Sippen Amt") of the Ministry of Interior, from where the case is sent to Dr. Abel's department for investigation. All persons involved are obliged to appear personally. In case of death or absence from the country, photographs may also be offered as evidence. They are very often found to be falsified by retouch.

There was the rather amusing case of a young girl. Dr. Abel had been searching for a good illustration of an Aryan woman for a new book. He finally selected a really lovely picture from the files of a popular photographer, who laughed out loud and said:

"There we see how much you scientists know. This girl is a Jewess."

Dr. Abel would not believe it. A few days later, the girl turned up in his office. The photographer had told her the story. Dr. Abel repeated that he believed her to be Aryan. So the girl went home and had a heart-to-heart talk with her Aryan mother, who finally burst into tears and told her that her real father was the brother of a French ambassador, and not her Jewish husband. The case was brought up through the regular channels, and all the detailed researches substantiated the admission of the mother.

A very able and highly respected high school teacher of mixed parentage made a similar effort. But, although his claim was supported by his Aryan mother, who produced a supposedly genuine Aryan father for her son, the extensive evidence permitted but one conclusion, that he was actually the son of his legal Jewish father. He of course lost his teaching job, and Dr. Abel added, as he put the case back in the file:

"I really felt awfully sorry for him. He was a good man."

Genetics really seems to have an unlimited field of practical applications, but I am sure that the old priest Mendel would have had the shock of his life had he been told that seventy-five years after he planted his unpretentious peas in the monestery garden of Brűnn, his new science would be called upon to "grade up" the "scrub" population of Greater Germany to new "standards of Aryan perfection." I am sure he would have damned his peas, or at any rate those who rediscovered them in 1900.

POLYPLOIDS IN THE GENUS CUCUMIS*

Preliminary Account

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THE family Cucurbitaceae includes representatives having 7, 10, 11, 12, 13, 16, and 20 chromosomes as haploid numbers.[6] The cultivated cucurbits; namely, *Cucumis sativus, Citrullus vulgaris, Lagenaria vulgaris, Cucumis melo,* and the genus *Cucurbita* have haploid numbers of 7, 11, 11, 12, and 20 chromosomes, respectively. Although cucumber and melon are of the same taxonomical genus (*Cucumis*), the former is the only species in the family having the lowest number of chromosomes ($n=7$), while the latter represents the modal chromosomal class of the family ($n=12$).

No spontaneous polyploids have been reported in this family; however, karyological studies reveal the general occurrence of polysomaty in the root-tips of the cultivated cucurbitis.[4,7,10] Kozukhow[8] was able to increase the number of polyploid cells in the root-tips and shoot apices of *Cucumis sativus* by subjecting its seed to relatively high temperature.

Following the discovery of colchicine as an important polyploid inducing agent in plants, Sinnott and Blakeslee[13] reported colchicine induced tetraploids of *Cucurbita pepo* ($n=20$) and *Lagenaria vulgaris* ($n=11$). In 1939 the writer started colchicine experiments with *Cucumis sativus*. Later on, some varieties of melons (*Cucumis melo*) were treated as well. Tetraploids of both cucumber and melon were obtained. The main objective was to study systematically the behavior of these autotetraploids and their possible practical value. The tetraploid cucumbers were grown under greenhouse and field conditions for five generations and only these forms are discussed in this paper.

Polyploidy in the Cultivated Cucumber (*Cucumis sativus*)

It was found that the treatment of the shoot apex at the cotyledon stage of growth with 0.3—0.5 per cent colchicine emulsion is the most efficient method for mass production of polyploids in the cucurbits. Gabaev[5] treated different varieties of cucumbers with colchicine and acenaphthene. He probably employed sub-threshold concentrations since only polyploid sectors were reported in his experiments. The treated plants may appear morphologically octoploid or higher polyploid in the early stages and thereafter they may revert to the tetraploid or diploid condition. Chromosome counts were made from root-tips to establish definitely the polyploid character of individual plants.

The varieties Abbott and Cobb (A & C), Early Russian, White Lemon, and Chinese Long were selected for the study because of their practical as well as genetical interest. These varieties vary in growth habit and in size, shape, color, spininess and hairiness of the fruit. White Lemon is the only andromonoecious variety in the group.

Tetraploids of the above four varieties manifest, in general, the expected tetraploid features. Under favorable greenhouse conditions (average temperature

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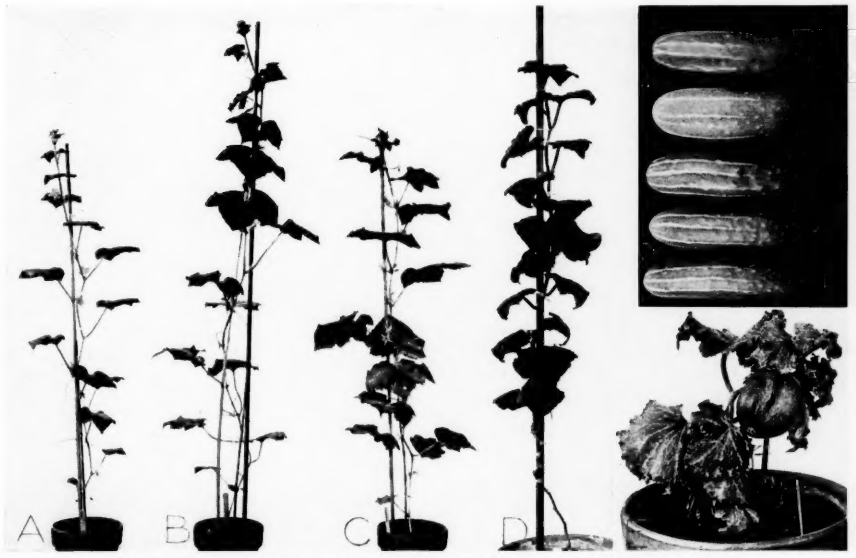


CUCUMBER PLANTS AND FRUITS OF THE VARIETY *A & C*

Figure 10

A-C—Three mature representatives of the first generation from seed obtained from colchicine treated plants. They are (*A*) a possible maternal diploid, (*B*) a tetraploid and (*C*) a tetraploid mutant. *D* is a typical tetraploid mutant of the second self generation. *E* is an old octoploid or higher polyploid plant. Note the spherical fruit. *F* shows fruits of this variety. The two lower fruits are diploids, the center fruit is a $2n$ fruit stimulated by $2n$ pollen. Only abortive seeds develop in such fruits. The two upper fruits are tetraploids of this variety. All are of the same age and stage of maturity. (Greenhouse studies.)

75° F. and long day) they are more vigorous, have thicker stems and petioles, and their leaves are thicker, darker in color, and slightly more hairy than those of their corresponding diploids. However, the most outstanding feature of these tetraploids is the accentuated serration of the leaf margin (Figure 11*A*). The general effect of chromosome doubling on flowers, fruit, and stomates is shown in Figures 10, 11, 12 and 13. The octoploid or higher polyploid cucumber of the variety A & C (Figure 10*E*) is very different from the diploid and tetraploid forms. Besides stunting of stature, the shape of the ovary is modified (Figure 11*B*) and the fruit differs from the typical elongate form of the diploid in being spherical or oval in shape. Although the corolla of the octoploid pistillate flower is slightly reduced, that of staminate flower is vestigial.

The relative size and frequency of stomates, the size of pollen grains and number of chloroplasts per epidermal cell

The stomates, chloroplasts, and pollen grains of the induced tetraploids were compared with those of the parental diploids. These studies were made from young tetraploid and diploid seedlings. Epidermal strips were peeled from the lower surface of the cotyledons at the same relative position in both the diploid and tetraploid plants.

It is concluded that the frequency of stomates per unit of area is decreased as a result of chromosomal doubling. This decrease is associated with an approximately equal increase in area of the tetra-

ploid stomates. The chloroplasts in the tetraploid cells are not larger in size than in the diploid cells, but the number is 1.6 times as great. However, since the area of the tetraploid cell is 1.6 times as great as that of the diploid, the number of chloroplasts per unit of cytoplasm in both tetraploid and diploid tissues remains the same.

The mean diameter of the diploid pollen is 1.3 times as great as that of the haploid pollen; the area is 1.8 times as great, and the volume is approximately 2.4 times that of the haploid pollen. However, if the diameter of the "balanced" diploid pollen only is considered, the approximate corresponding ratios are 1.4, 2.0, and 2.9, respectively.

Shape and Size of Fruit

Sinnott and co-workers[13, 14, 15] reported that the tetraploid fruits of *Lagenaria vulgaris* and *Cucurbita pepo* were not larger in size but rather were shorter and broader than were their corresponding diploids. The ovaries of one 4*n* line were actually larger than the diploid, but they failed to maintain this advantage during development. As will be shown later, the tetraploid cucumber, in comparison with diploid, has a reduced ecological range for optimum growth. Under favorable greenhouse conditions for the growth of some of the tetraploid varieties the fruits are more truncate but are not appreciably shorter, if at all, than the diploid fruits (Figure 10*F*). The same tetraploid varieties will produce markedly shorter and broader fruits than the diploids under field conditions at Ithaca, New York. In contrast to this reaction, other tetraploid cucumber and melon varieties produce consistently shorter fruits under wide variations of environment. In the latter case the shorter fruits are not wider than their diploid fruits, and therefore, the increase in width of fruits is not an inevitable change associated with tetraploidy.

The change in shape or size of the tetraploid fruit may be already established in the early stages of ovary development. However, it may still be modified during fruit development. The ovary length of the typical tetraploid mutant is as long as that of the normal tetraploid, but during fruit development the length is suppressed, resulting in a distinctly shorter fruit (Figure 14). In the case of the octoploid or higher polyploid forms, the ovary (Figure 11*B*) is wider and slightly shorter than that of the tetraploid. The ripe fruit of the former is spherical or ball shape (Figure 10*E*) and much smaller than either the diploid or the tetraploid fruits.

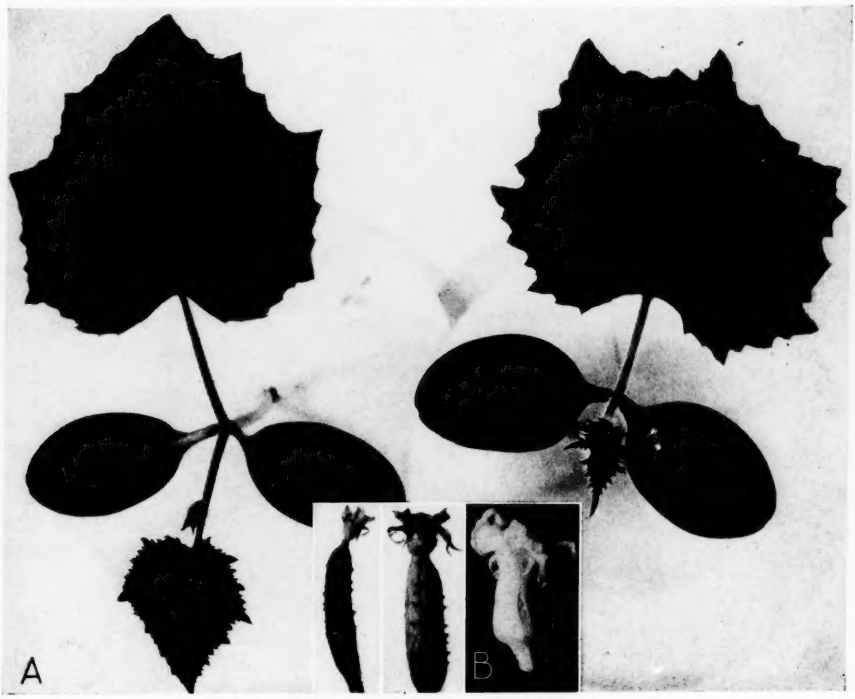
These changes in fruit shape and size cannot be attributed to the progressive decline in the production of viable seed of the polyploid series in the cucumber. It has been found that seed production in the cucumber is not an essential requirement for normal fruit development. Diploid fruits from $2n \times 4n$ crosses are normal in size and shape (Figure 10*F*) although they contain no viable seed in the majority of these cases.

Since different species and varieties may react in different ways to chromosome doubling in respect to changes in shape and size of fruit, it is assumed that these changes have a genetical basis. Although chromosome doubling supposedly is not concerned with gene mutation, it does probably affect the genic action and the relationship between various genes in the new genetical systems produced. However, in attempting to interpret the changes in shape and size of fruit one may have to consider not only the initial genetical patterns and the level of chromosome multiplication but the physiological reaction of the polyploid plants as well.

Maternal Diploids

In the first, second, and third generations of the tetraploid population occasional diploids were recovered at the seedling stage. Thus, in the second selfed generation of the tetraploid variety A & C there were six diploids in a population of 800 tetraploid plants.

Reported cases of autopolyploid reversion from the tetraploid to the diploid condition are rare. Nilsson[9] described diploid derivatives of *Oenothera gigantea,* and Randolph and Fischer[12] presented conclusive evidence that the relatively frequent occurrence (1:1000) of diploid plants in autopolyploid corn was



SEEDLINGS AND OVARIES

Figure 11

A—Seedlings of a diploid (left) and a tetraploid (right) showing early differences. Note the characteristic serration of the tetraploid leaves. (2/3 natural size.) *B*—Ovaries of diploid (left), tetraploid, and octoploid (right), showing the change in shape of these polyploid floral structures.

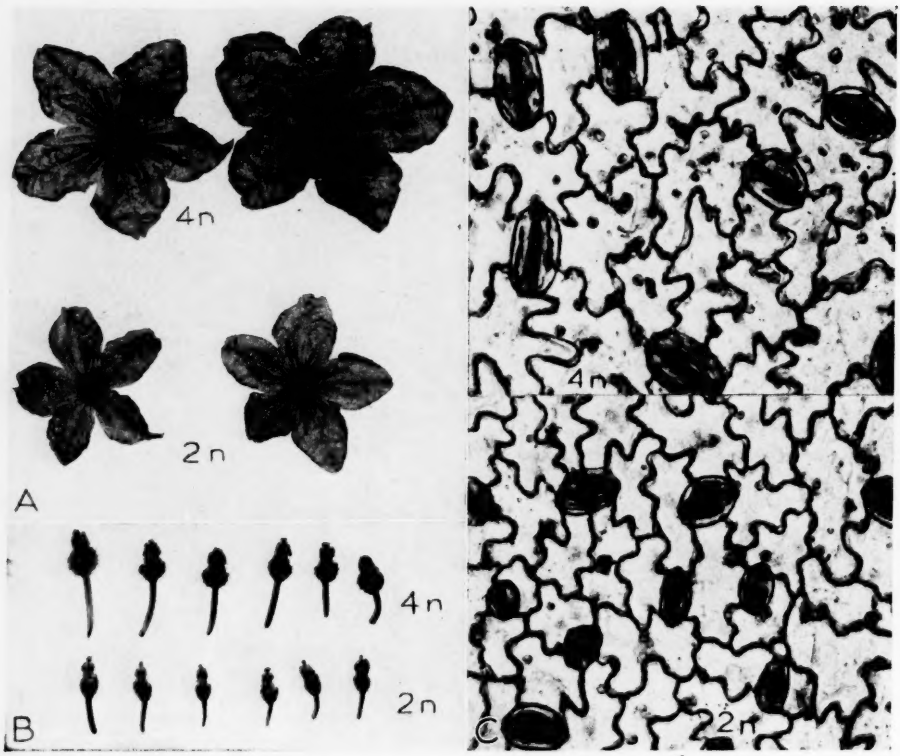
due to parthenogenesis. The above diploid derivatives of tetraploid cucumbers were assumed to be of maternal origin but this was not definitely confirmed by genetical test.

Mutant Segregates

Randolph,[11] Eigsti,[2,3] and others reported that heat treatment and colchicine may cause chromosome aberration or abnormal nuclear variations in addition to chromosome doubling.

The colchicine treated plants in these experiments manifested a variety of morphological abnormalities which, in part, could be attributed to some direct plasmatic stimulation exerted by the alkaloid. However, in the succeeding selfed generations of the tetraploid population typical mutants were recovered. Thus, one mutant (Figure 10*C*) although deviating slightly in its general appearance from the normal tetraploids, was self-sterile and when cross-pollinated gave considerably larger seeds than the normal tetraploid. Typical mutants (Figure 10*D*) appeared in the second and the third generations which actually did not resemble cucumber plants from their early growth. They were entirely sterile. Some normal tetraploid segregates in the third and fourth generations had white-colored fruits instead of the green fruits of the diploid stock.

The fact that these mutants were noted only in later generations and did not appear in the first generation suggests that recessive mutation, chromosomal or



SIZE DIFFERENCES IN DIPLOID AND TETRAPLOID STRUCTURES
Figure 12

Staminate flowers (*A*), corolla removed (*B*), and stomata (*C*) of comparable diploid and tetraploid material.

genic, had occurred. In addition to these distinct mutants one tetraploid segregate was found to be more vigorous and to bear definitely larger fruits than that of the normal and diploid (Figure 12). However, the origin of this segregate may be due to the initial heterozygosity of the diploid stock. Small genetical differences may not be distinguishable in the diploid stage but may be pronounced or accentuated in the tetraploid condition.

Physiological and Pathological Reaction of the Tetraploids

Experiments with the tetraploids and their parental diploids were conducted both in the greenhouse and in the field. The data taken from the greenhouse studies (temperature 75°F.) indicate that the growth curves of the tetraploid plants generally follow quite closely the growth curves of their corresponding diploids. The tetraploids were not later in the production of staminate flowers but were later than the diploids from 8 to 14 days (depending on the variety) in the production of pistillate flowers. The length of the life cycle was approximately the same in both tetraploid and diploid plants.

Under conditions of relatively low temperature in the field the growth of the tetraploids was markedly retarded, internodes were shortened, branching was inhibited, the life cycle was presum-

ably longer, and plants were from 30 to 40 days later in maturity than diploids. The above striking difference in growth performance of the tetraploids under different environmental conditions suggests that they have different physiological norms as well as a reduced geographical zone for optimum growth.

There is also evidence that the tetraploids are more sensitive to mild frost (probably because of greater content of unbound water) and at least just as susceptible to most common cucumber diseases as are the diploids.

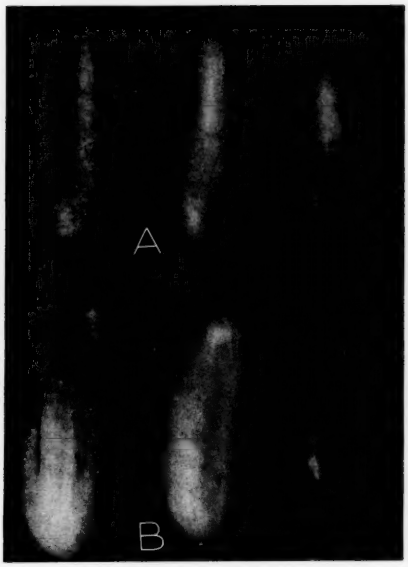
Fertility of the Induced Tetraploids

All the treated plants manifested a remarkable degree of sterility. This was true of plants grown in the greenhouse as well as of those grown in the field. Both the number of viable seed, five per cent of the diploid, and total number of seed (including abortive) per fruit were markedly reduced. The high sterility in the treated plants may be due to the indirect effect of the alkaloid on the vigor of the plants, to the presence of periclinal chimeras, or to some other unknown causes. These factors were eliminated in later generations since there was a pronounced increase of seed production.

In some of the treated plants, as well as in those of the first generation from seed, pollen grains germinated occasionally in the anthers before pollination. It could not be ascertained whether this premature germination contributed to any degree to the high seed sterility of the treated plants. Pollen fertility* of the tetraploids may range on the average, under favorable conditions, from 65 to 85 per cent, depending on the variety. However, it is realized that variability in the fertility of single tetraploid plants is also very great. While fertility of the haploid pollen may vary from 85 to 99 per cent in the same diploid plant, the diploid pollen under the same circumstances may vary from 40 to 85 per cent.

Additional studies on the same subject suggest that pollen abortion may not only increase after anthesis but also that wide variations occur in the young flower buds. Further studies are essential for determining the factors involved but it may be suggested that the tetraploid plants are more senstive to unfavorable environmental factors, especially temperature, which have a direct effect on pollen fertility. Such factors may increase meiotic irregularities or may adversely affect the potency of the diploid pollen grains and especially those of "unbalanced" constitutions.

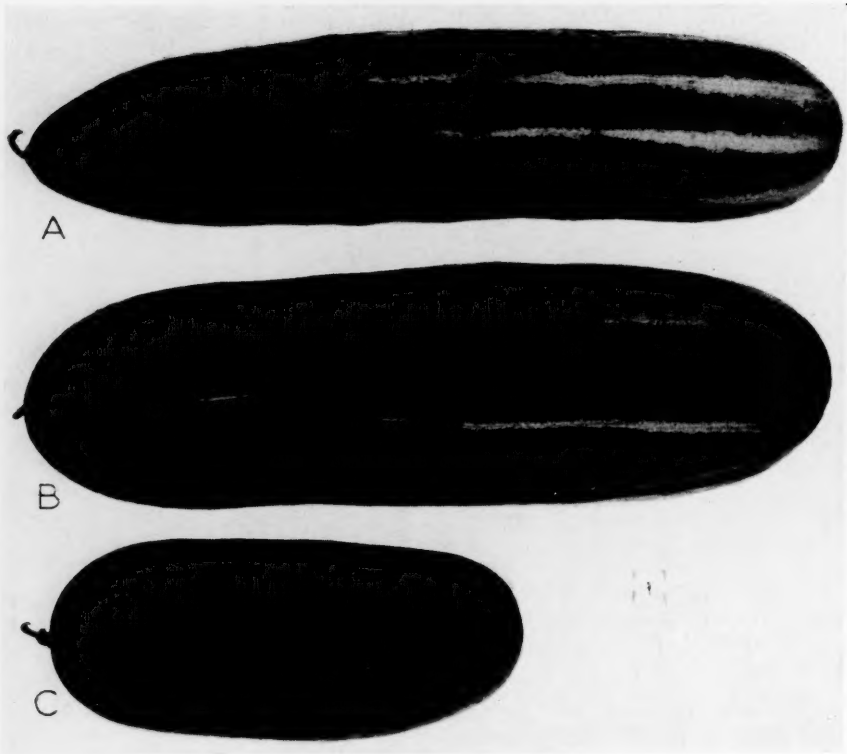
Associated with pollen variability, there is also extreme variability in seed production in fruits of individual tetra-



FRUITS OF EARLY RUSSIAN VARIETY
Figure 13

Diploid (*A*) and tetraploid (*B*) fruits of comparable stages of development. The tetraploid fruits of this variety may resemble the diploid in size and shape, but they do not tend to be tapered at both ends as the diploid do. They have relatively larger scars at the blossom end. The teraploid fruit at the extreme left is actually longer and broader than any of the diploid fruits. It came from an exceptionally vigorous segregate. (Greenhouse studies.)

*The terms *fertile* and *sterile* pollen are inaccurately used here for plump and shrivelled pollen.



FRUITS OF VARIETY A & C

Figure 14

Normal (*2n*) fruit (*A*) and tetraploid (*4n*) fruit (*B*) which shows some cracking of the rind; and *4n* fruit (*C*) from the typical mutant segregate (Figure 10*D*). All are at the same stage of maturity. Greenhouse material. (2/5 of natural size.)

ploid plants, even under relatively favorable conditions. From the practical standpoint it may seem significant that 100 to 140 viable seed were obtained from fruits borne on different tetraploid plants, the average number of diploid seed per fruit is 160. However, the very same plants produced fruit which contained 16, or no viable seed at all. Such variability greatly exceeds that which occurs in the diploids under the same environmental conditions.

Although it is possible to isolate tetraploid segregates which will differ consistently in degree of seed fertility, all the tetraploid varieties are highly sterile under field conditions, Ithaca, New York 1939, 1940, and 1941. Production of viable tetraploid seed under greenhouse conditions may range from 50 to 60 per cent for the most fertile stocks while under field conditions it will not exceed 15 per cent of that of the corresponding diploid.

The decrease in seed production may also be due, in some cases, to initial decrease in the total number of ovules produced in the tetraploid ovaries. Thus, whereas the total amount of seed, including abortive, per fruit in the tetraploid variety A & C was at least equal to the amount in the diploid form, the

total amount of seed per fruit in the tetraploid variety Early Russian was less than 50 per cent of the diploid.

The following factors are suggested as playing important roles in the sterility of the autotetraploid cucumber:

1. The chromosome irregularities which result in certain percentage of shrivelled pollen and abortive eggs.
2. The supersensitivity of the $2n$ pollen to relatively minor temperature fluctuations.
3. The production of undersized embryos which fail to develop under ordinary conditions.
4. The initial genetical constitution.
5. The possible reduction of the total number of ovules produced in the tetraploid ovaries.

However, the physiological reaction of the tetraploid plant as a whole is by far the most important contributing factor for high sterility under adverse field conditions.

The data also afford additional evidence that autotetraploid derivatives of species having low numbers of chromosomes of small size are not necessarily more fertile. *Cucumis sativus* with only seven chromosomes and these small, has highly sterile autotetraploid derivative.

Intercrosses Between Diploid and Tetraploid

In general the data pertaining to crosses $2n \times 4n$ and $4n \times 2n$ are comparable with those obtained in other plant species. The cross $2n \times 4n$ yielded 0.05 per cent of viable seed and the $4n \times 2n$ cross 1.11 per cent of viable seed. The greater percentage of supposedly viable seed obtained from the $4n \times 2n$ cross is probably not of great significance since the embryos of these seed are exceedingly weak. Thus, once they are established the tetraploids represent a distinctly isolated population.

Spontaneous Tetraploids

In searching for natural tetraploids in untreated material *one* such plant was discovered in a field composed of some 25,000 diploid seedlings. Because of disease infection the plant could not be saved for propagation. Its morphology was very similar to that of the artificially produced tetraploid. Pollen fertility amounted to 80 per cent.

Summary

1. Colchicine-induced tetraploids of the cucumber, *Cucumis sativus,* exhibit, in general, the expected gigantic features. However, the accentuated serration of the leaf margin is their most distinguished peculiarity.

2. It is interesting that only in the octoploid or higher polyploid forms do we find a pronounced difference in the size of the corrolla between staminate and pistillate flowers borne on the same plant.

3. In the succeeding selfed generations of the tetraploid population maternal diploids, typical mutants and segregates for plant vigor, size, and color of fruits, were recovered.

4. The frequency of stomates per unit area is decreased by chromosome doubling but the frequency for a given number of epidermal cells is the same in both the tetraploid and diploid forms.

5. The size of the chloroplasts and the number of chloroplasts per unit of cytoplasm are not significantly different in the diploid and the tetraploid forms.

6. The dimensional change in fruit shape brought about by polyploidy depends apparently on the initial genic patterns involved, the level of chromosome multiplication, and in some cases, on the physiological reaction of the tetraploid plants. The type of change in fruit shape may be interpreted on the basis of modified genic action in the genetically new systems produced by chromosome doubling.

7. The tetraploid cucumbers possess new physiological norms. They actually have a reduced range of ecological adaptation and are at least as susceptible to most cucurbit diseases as are the diploids.

8. Fertility in the cucumber is affected by environmental factors. Sterility as a character is accentuated by chromosome doubling due to the physiological reaction of the tetraploid plants and the initial increase of pollen and egg abortion. The interaction of several possible factors is discussed.

9. Intercrosses between diploids and tetraploids are extremely difficult to obtain, suggesting that once they are established the tetraploids represent a distinctly isolated population.

10. It has been demonstrated that spontaneous tetraploids do appear at a low frequency in the cultivated cucumber. However, a natural tetraploid population can hardly exist under the present environmental conditions.

Several autotetraploid vegetables (beet, broad bean, cabbage, cucumber, lettuce, melon, potato tomato, squash, etc.) have been produced by various workers. However, these forms do not represent, at the present time, new types that are commercially superior. They are of recent origin and it is possible that marked improvement may be achieved by breeding.

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PROMETHIAN FIRE

IN these days which try men's lives, it is important that we have clear and accurate evaluations of the things men live by. Man lives by fire as well as bread, — the fire of Prometheus, and the knowledge juice—squeezed from the apple which Eve picked. So that the juice will not corrode, and the fire not burn down the house of our human culture, it is important that all free men understand the basis of human thought-processes, and the steps whereby men have come to their 1942 estate. Dr. Albert Ramsperger of the University of Wisconsin presents a timely and excellent review* how the human mind has marched toward an understanding of reality from the days of the Greeks and before to the days of Mendel and Wundt and Einstein.

Democritus discovered that things are not what they seem. During the next 2500 years the path of human thought has been littered with the wrecks of bogus conceptual structures built out of false and misinterpreted sense-perceptions. There is also another side of the picture which Ramsperger fails to do justice to and that is the endless war of those who prefer to make their universes out of the whole cloth of introspection, bolstered with the seal of intuition and inspiration. This is touched on casually, but the reader does not get the idea that there is a continuing battle to the death between the "learn hows" and the "know hows". On the one side is the army of Science composed of those who try to learn of the Universe and life by finding out the rules which govern the nature of things, opposed by that still formidable army of those who claim to know *ad hoc* how the universe works. Bruno burned a bit casually, and Galileo is pictured as working out the handling of data in a vacuum almost as complete as that in which all objects fall with equal

(*Continued on page* 160)

A PALE VARIATION IN A GROUND SQUIRREL

Notes on A Pale Individual of the Thirteen-Striped Ground Squirrel *Citellus Tridecemlineatus Tridecemlineatus* (Mitchill)

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A CAPTIVE female thirteen-striped ground squirrel, *C. tridecemlineatus tridecemlineatus,* gave birth to a litter of six young at Lincoln, Nebraska, on May 15, 1940, at the Irving Junior High School Science Museum, and was accidentally killed 15 days later. The orphaned litter was brought to the Department of Zoology, University of Nebraska, on June 1, at which time it was noted that one of the six young squirrels was markedly pale, the remaining five showing typical coloration. They were fed on warmed, diluted cow's milk for two days. On June 3 a wild female ground squirrel in lactation was captured alive. Offered one of the young squirrels, she accepted it, after which she was given the entire litter.

Three females of this litter have been raised to maturity, with attention centered upon the pale individual which is shown in upper figure with a wild female of typical coloration taken at Lincoln on October 5, 1940, and in lower figure with one of her litter mates, also a typical, dark female. The photographs were taken on August 7, 1941.

Microscopic examination of hairs from this pale specimen, as compared with hairs from her litter mates and other squirrels of this subspecies taken at Lincoln, shows (1) the dark pigment generally less concentrated in both the varigated or banded hairs and the entirely dark hairs; i.e., whereas a dark guard hair of a typical colored individual appears almost black by reflected light, that of the pale squirrel is smoky brown; and (2) in the varigated hairs the dark band is relatively shorter. This is especially noticeable in the lateral hairs of the tail in which the dark band is much reduced and the dark tip is lacking. This decrease in density and area of dark pigment within the individual hairs results in lessened contrast between the base color (about Natal Brown* to about Snuff Brown) of the dark longitudinal stripes and the buffy gray (about 11 A 1†) of the light longitudinal stripes, and appears to be chiefly accountable for the pale coloration which was noted in the 17-day-old squirrel and has persisted into adulthood. The light stripes of the pale individual and of the typical, dark squirrels show little or no difference in color, the marked difference appearing principally in the dark stripes, those of the typical squirrel being about Warm Blackish Brown to about Bone Brown.

The dark dorsal stripe of the pale specimen of *C. t. tridecemlineatus* is strongly admixed with buffy-gray, thereby nearly losing its identity, especially posteriorly, approaching throughout its length the "peppered" appearance commonly seen in the dark stripes of *Citellus tridecemlineatus pallidus* of more western occurrence. The other dark longitudinal stripes of the pale individual have the base color uniform, i.e., lacking the admixture of buffy-gray hairs. The lateral line of the pale specimen has retained the buffiness (Pale Pinkish Buff to Pinkish Buff) of typical *C. t. tridecemlineatus,* showing no approach to the whitish (about Ivory Yellow) of the lateral line

*Named colors are those of Ridgway.[4]

†Colors designated by number and letter symbols are those of Maerz and Paul,[3] *Dictionary of Color* (1930).

A PALE MUTATION

Figure 15

Above—Thirteen-striped ground squirrels, *Citellus tridecemlineatus tridecemlineatus* (Mitchill). The pale female, born in captivity, is to the left; a wild female, showing coloration typical of the subspecies, is to the right. *Below*—Thirteen-striped ground squirrels, *C. t. tridecemlineatus*. The pale female is to the right, her normal colored litter mate to the left.

of *C. t. pallidus* which has buffiness limited for the most part to the mantle and flank regions. The mantle, muzzle, and flank regions of the specimen here reported are about Cinnamon Buff, the muzzle being nearly free of the admixture of blackish hairs seen in the typical individuals, the tip of the nose, lips, chin and throat being almost white, as in *pallidus*. The top of the head is markedly lighter in color than in typical specimens of *tridecemlineatus*, tending toward buffiness. The toes are whitish and the claws are without pigment, typical, dark squirrels having claws dark at the base.

Temperamental Differences

Clark and Jellison[1] have reported the collection of pale individuals of *Citellus elegans* in Beaverhead County, Montana, in the summers of 1935 and 1936. They observed these pale squirrels, which they considered as mutants, as being more tractable than the normal colored speci-

mens immediately after capture, and quite docile after a short confinement. It is of interest to note here that the pale specimen of *C. t. tridecemlineatus* has been at all times tractable, readily submitting to handling, whereas her two sisters have exhibited unpredictable dispositions, even being aggressively pugnacious.

The occurrence of a pale individual in an otherwise typical colored litter of thirteen-striped ground squirrels suggests the condition noted by Dobzhansky.[2] Speaking of the "appearance of aberrant individuals among masses of normal representatives of a species in nature," he states that "in a number of cases it has been established with varying degrees of certainty that aberrations of this sort are in reality hereditary types, mostly recessive to the normal condition, the rare instances when the recessive genes, long carried in the population in heterozygous state, emerge as homozygotes because of the occasional mating of two carriers."

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A POSSIBLE PATERNAL FACTOR IN THE ETIOLOGY OF MONGOLISM

S. J. Lipnitzky, M.D. and Benjamin Boshes, M.D.

THE etiology of mongolism has always been a controversial subject. Many writers have stressed maternal factors, e.g., advanced age or faulty endocrine glands which might impair the vitality of the ovum.[1,6,12] The emphasis has been on the female only, and although the spermatozoon has occasionally been considered,[5] usually it has not been taken into account at all.[9] Hereditary influences which might have played a role in the production of a mongol have been denied by some,[9,10] but emphasized by others. Jenkins[6] pointed out that when mongolism appears in monozygotic twins, both are affected. Tatafiore[11] reported mongolism as a family characteristic. A baby and a maternal aunt had presented the typical picture. Fantham recorded ten cases of mongolism in three generations of one family.[4] Southwick[10] objects to the hereditary theory on the basis that multiple cases in one family are rare. Doxiades and Portius found only 50 cases in the entire literature.[3] In 2,491 families with mongolism Macklin[7] found only 30 instances of more than one case. Southwick states that so few cases speak against a hereditary factor. Turpin and Caratzali,[13] however, studying antecedents and collaterals of mongols found them to have many individual characteristics such as a fissured tongue. He considers these as "forme fruste" cases of mongolism, and the conditions as genetically determined. Pogorschelsky[8] and Chotzen[2] each reported an instance where two sisters had borne mongolian children, suggesting a maternal factor.

In the Dixon State Hospital, we recently had occasion to record two cases of mongolism, where the patients, a male and female child were first cousins. In this instance the fathers were brothers and the mothers were not related. The age of the latter at the time of birth of the children was 27 and 30 years respectively and both patients were second in order of birth. There was no history of pathological pregnancies, such as miscarriages, stillbirth, or premature birth. The mothers were married at 22 and 23 years of age respectively and both seemed to be in good health. The only common factor in the two cases was the fact that the fathers were brothers.

Report of Cases

Case 1.—P.S., a white male infant of 17 days was admitted to the Dixon State

Hospital on June 10, 1939. Both parents were born in 1909, were of good health, had married at the age of 23 years, and were 30 years old at the time of birth of this patient. The mother had had no miscarriages, no stillbirths, and no premature births. Her health during the pregnancy was excellent. Both parents were said to be bright and except for cancer, the hereditary history was negative. The patient's birth occurred on May 24, 1939, labor lasting for five hours. Ethylene gas anesthesia with forceps was used. The pregnancy was full term, the baby weighing 5 lbs. 3 ounces. He was diagnosed by several physicians as a "mongolian idiot" prior to his admission to the Dixon State Hospital. He has a brother of 5½ years, who is regarded as bright and in perfect health.

The physical examination at the Dixon State Hospital revealed a 17-day-old male child whose features were mongoloid. The circumference of the head measured 13 cms. He had a round face and small ears. It was thought that he might have a congenital heart malformation because of occasional spells during which his face would turn blue and he would have difficulty in breathing. The laboratory workup was essentially negative. Since admission the child suffered from diarrhea and on November 4, 1939, he expired, death being attributed to chronic gastroenteritis and mongolism.

Case 2.—A.S., a white female infant of four weeks of age was admitted to the Dixon State Hospital on October 19, 1939. The father was the brother of the father of P.S. Both parents of A.S. were born in 1911, married at the age of 22, and were 27 years old at the time of birth of this child. The parents were said to be bright and in good health. The mother had no pathological pregnancies. The patient's sister of 3½ years was in perfect health. According to the father: "the older brother had had a mongol baby born to his wife five months ago." The patient was born on September 18, 1939, second in order of birth and a full term child. The health of mother during the pregnancy and labor was good. The baby weighed 6 lbs. A week later, the doctor told the parents that the baby was a "mongol."

The physical examination at the Dixon State Hospital revealed a four weeks' old female child whose features were mongoloid. Right external strabismus, ptosis of the upper left eyelid, and a deep furrow between the first and second toes of both feet were noted. The circumference of the head measured 13 cms., her face was round, breathing oral, and the heart sounds were accentuated at the apex. On the right side, a Babinski reflex was present. The laboratory examination was essentially negative.

The mongoloid features mentioned above were apparent in both cases. The occipital protuberance, the face, and the bridge of the nose were flattened. The palpebral fissures appeared oblique and narrow, and a fold of soft skin was raised slightly over the upper eyelids at the inner canthus. Occasionally the tongue would protrude from a small oral cavity, and the little fingers had a tendency to curve-in medially.

Conclusions

1. Two cases of mongolism where the patients were first cousins were seen at the Dixon State Hospital.
2. Further studies on the role of the father in the etiology of mongolism are recommended.

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THE DETECTION OF LINKAGE

IV. Lack of Parental Records and the Use of Empirical Estimates of Information

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IN spite of the multiplicity of methods which have been presented for the study of linkages between human genetic traits, very little evidence in favour of linkages has so far been obtained[4,5,7,16]. Bearing in mind the labor involved in obtaining family material suitable for linkage studies, it is clear that it is of the greatest importance to make efficient use of all relevant data.

Snyder[22] in 1926 recognized the necessity of examining separately each family for cross-overs and non-cross-overs in records covering two generations, but it was not until 1931 that Bernstein[1] developed a sound method both for the testing of the existence of linkage and the estimation of recombination. His principles were adopted by Wiener[25], Hogben[17,18], and Haldane[15]. Fisher[10-13] developed further his new and fundatal technique in a series of papers which introduced the concept of efficient scores, extracting from each family all available information relevant to the existence of a linkage. The use of these efficient scores has since been extended and systematised so as to cover more complex mating tvpes.[6-9] Mather and Philip[19] have derived modifications appropriate to genes variable in their manifestation on account of having less than 100 per cent penetrance.

The possibility of utilizing records of one generation only was realized independently by Snyder, by Burks[3-5], and by Penrose[20,21]; the latter showed how the recombination fraction might be estimated from such data if the gene frequencies in the general population were known. The methods of all these workers were essentially the same. In their application it has, unfortunately, often been forgotten that knowledge of one or both parents in respect of the traits studied adds considerably to the value of records, and that much of the available information on linkage is lost if such knowledge is ignored. This has recently been shown[8,9] in the case of data collected by Boyd[2].

It is now possible to extend the principle of efficient scoring systems to family records from which one or both parents are completely lacking. The present note illustrates this new technique on Boyd's data and on data presented by Snyder in a recent issue of this JOURNAL[24].

The Scoring Technique

It has been shown in Part I of this series[6] that every family of known parentage provides an efficient score, λ, for the detection of linkage, and Table I of that paper lists, for simply allelomorphic characters, all parental combinations giving non-zero scores. The variance of such scores is obtainable from other tables of the same paper. A more general theorem, given in Part III[9], states that, when lack of knowledge in respect of one or both parents leaves some doubt as to the parental genotypes, the efficient score is the sum of the products of the scores corresponding to each possible mating which could show crossing-over amongst its offspring with the corresponding probabilities that these matings were the true ones. Such probabilities may be estimated from the phenotypes of the children and of any other relatives who may be known; formulae, based on the children only, are given in the paper. When parental descriptions are incomplete for one factor only theoretical variances of the scores may be obtained analagous to those of Part I, but when both characters are in some measure incompletely described an empirical estimate of variance must be used.

For the purposes of the present paper it will be assumed that the population frequencies of the M and N blood type genes are equal, and also that the fre-

quencies of T and t, the dominant and recessive genes for P.T.C. reaction, are equal. These are in reasonable agreement with the estimates given by Snyder[23] for an American population and are probably not greatly in error even for the races studied by Boyd; inaccuracy in these estimates will to some extent lower the efficiency of tests based on them, but this effect will be small and no bias is introduced. Table I shows the probabilities, on this basis, that a family of x tasting and y non-tasting sibs should have had either $Tt \times tt$ or $Tt \times Tt$ parents; mating of homozygous tasters or of two non-tasters have, of course, no interest for linkage. A similar table has been drawn up to show the probabilities that a family of x M, y MN and z N sibs should have had $MN \times M$, $MN \times MN$, or $MN \times N$ parents, but this is not reproduced here.

Using these two sets of probabilities, the possibility of linkage between the MN agglutinogens and the P.T.C. reaction may be tested on Snyder's 64 sibships[23]. For example family 8 has two M and two MN children; the probability that the parents were $MN \times M$ is therefore 0.8 and that they were $MN \times MN$ is 0.2, $MN \times N$ being impossible. All these children were non-tasters and from Table I the two matings of interest have probabilities 0.1975 and 0.0123. The probability that the parents were actually $MNTt \times Mtt$ is therefore $\frac{1}{2} \times 0.8 \times 0.1975 = 0.0790$; from Part I the linkage score of this sibship from such parents would be —2 and thus the contribution to the score from this possibility is —0.158. Adding similar contributions for matings $MNTt \times MNtt$, $MNTt \times MTt$, and $MNTt \times MNTt$, the total score of —0.266 is obtained. Table II shows the family size, s, and the score λ, for the 16 sibships with more than two members. The families with $s = 2$ give a total score of —2.807, details of which are not shown here.

The Information Extracted

It has been demonstrated[6,9] that the variance of a total linkage score is also the information* given by that score with respect to $[\ 1\text{-}4\chi\ (1\text{-}\chi)\ ]$, where χ is the recombination fraction, and that an estimate of this quantity, $(1\text{-}4\chi)$, is obtained by dividing the total score by its information content. For the 48 families of 2 this variance may be estimated empirically from the sum of squares of deviations of the scores and is found to be 1.482. Modifying slightly a suggestion of Fisher's[11], the variances of scores for the larger families may be assumed approximately proportional to $\frac{1}{2}s\ (s\text{-}1)$, and these 16 families pooled in order to estimate the variance of the total score. The variance of $\lambda\sqrt{\frac{1}{2}s\ (s\text{—}1)}$ is 0.03103, and this multiplied by 142 gives 4.406 as the variance of the total score. As the total score for the 64 families, —7.960, is negative there is clearly no indication of linkage. The total information, i, is 5.888.

TABLE I. Probabilities that a family of x tasting and y non-tasting sibs should have had Tt x tt (first entry) or Tt x Tt (second entry) parents.

x \ y	0	1	2	3	4
0	0.8500 0.9500	0.6000 0.8500	0.4444 0.7111	0.3200 0.6400	0.1471 0.5143
1	0.1667 0.2500	0.5714 0.7857	0.7273 0.9091	0.8421 0.9579	0.9143 0.9857
2	0.0476 0.2195	0.4706 0.8294	0.6400 0.9600	0.7805 0.9805	0.8767 0.9833
3	0.0244 0.1837	0.3721 0.8279	0.5424 0.9576	0.7273 0.9697	0.8353 0.9748
4	0.0294 0.1765	0.2432 0.7568	0.4474 0.9286	— —	— —
5	0.0156 0.1176	0.2286 0.7915	0.3750 0.8550	— —	— —
6	0.0080 0.0616	0.1494 0.7506	0.2699 0.7401	— —	— —
7	0.0041 0.0706	0.1048 0.8952	0.1807 0.8103	— —	— —

N.B. P_T is the probability that a particular parent is the Tt.

TABLE II. Scoring of Snyder's sibships for MN x Tt linkage test (sibships with only two members omitted).

Sibship	s	λ	½s(s-1)	λ/½s(s-1)	1/½s(s-1)
1	9	-1.437	36	-0.040	0.0278
2	8	-0.480	15	-0.032	0.0667
3	6	-0.977	15	-0.065	0.0667
4	5	0.829	10	0.083	0.1000
5	5	-0.490	10	-0.049	0.1000
6	4	-0.790	6	-0.132	0.1667
7	4	-0.131	6	-0.022	0.1667
8	4	-0.266	6	-0.044	0.1667
9	3	0.057	3	0.019	0.3333
10	3	0.041	3	0.014	0.3333
11	3	-0.076	3	-0.026	0.3333
12	3	0.057	3	0.019	0.3333
13	5	0.024	10	0.002	0.1000
14	3	0.057	3	0.019	0.3333
15	4	-1.061	6	-0.176	0.1666
16	3	-0.586	3	-0.196	0.3333
Totals	71	-5.153	142	-0.543	3.0611

TABLE III. Test of MN x T linkage on Boyd's and on Snyder's data.

Knowledge of parental phenotypes	No. of cases	No. of sib-pairs	λ statistics (1-4χ)	λ	Penrose technique (1-4χ)	1
Both [Boyd]	20	66	0.065	7.265	-1.338	0.510
One "	25	99	-0.027	9.837	-1.114	0.722
Neither "	123	218	-0.722	4.620	-1.023	2.645
Total "	168	383	-0.144	21.722	-1.081	3.877
Neither (Snyder)	48	160	-1.352	5.888	-0.492	4.050

TABLE IV. Theoretical information per family for families of size 2.

Knowledge of parental phenotypes	Information per family in linkage test of Sex x MN	Sex x T	MN x T
Both	0.3125	0.1308	0.0850
Father only	0.2188	0.1071	0.0477
Mother "	0.2083	0.0952	
Neither	0.1167	0.0598	0.0276
Sib-pair technique	0.0417	0.0226	0.0122

*The "information" given by a statistic is here used in Fisher's sense[14] as the reciprocal of the variance of that statistic; quantities of information from independent data are additive.

It was shown in Part II[8] that an estimate of the information yielded by the Penrose sib-pair technique could also be made. For this purpose the blood types are treated as a graded character, *MN* being intermediate between *M* and *N*, and a single analysis of pairs of sibs made, instead of the separate treatment of the two alleles given by Snyder. The information from the 190 pairs of sibs is 4.059; thus the loss from inefficient scoring is 31%. This loss in information is considerably more marked in the case of Boyd's data, which have been similarly examined, on account of the rejection of the knowledge of parental phenotypes in many families. The results are summarized in Table III.

In a test for sex linkage the use of the sib-pair technique will in general be less efficient than for autosomal linkages, as some knowledge of parental genotypes is inevitably discarded. Snyder's data have been tested by λ scores for sex linkage of the *MN* agglutinogens and 30.681 units of information were obtained as compared with 5.907 by the Penrose method; a similar test for the taste reaction gave 21.084 units instead of 4.925 by sib-pairs. There was, of course, no positive evidence for linkage. The same analysis applied to Boyd's material showed correspondingly large reductions in efficiency of utilization of the records when a sib-pair test was made[9].

It is, of course possible to use the efficient technique for tests with the *ABO* blood groups, but here the parental combinations are more numerous and their probabilities correspondingly more complex. For data in which there is any likelihood of discovering a linkage it would undoubtedly be worth while to use the efficient technique, particularly as a sib-pair analysis requires separate treatment of the *A* and *B* alleles and a consequent uncertainty as to how the results may be combined, but neither Boyd's nor Snyder's data have yet been analyzed in this way.

It is hoped to discuss more fully in a forthcoming paper methods for the derivation of the expected quantity of information per family in these various tests. Some results which have already been obtained for families of two are shown in Table IV. From these it is clear that, even when no parental descriptions are available, over 50% of the information is liable to be lost if the sib-pair technique is used, and this loss may be increased to 85% when both parents are known. These proportionate losses probably become larger with increasing family size, since the knowledge of the sibs will give increasingly good estimates of parental genotypes.

Summary and Conclusions

Fully efficient methods for the detection of genetic linkage in human population are now available even for data which consist of sibships only. Though the computational time required is considerable, the great increase in precision of the results repays the additional labor involved in using this technique instead of that of paired sibs. Data from two recently published collections of family material illustrate this conclusion in showing the sib-pair method to utilize in one case only 70% and in three other cases only about 20% of the information given by the efficient technique. Theoretical investigation shows that even when no parental descriptions are available the sib-pair technique can only be expected to be about 50% efficient and that this figure is much reduced when records of the parental generation can be used.

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Promethian Fire

(*Continued from page* 152)

velocity, rather than whispering, in the shadow of the stake, "It still moves."

It is perhaps an unfair criticism of an outstanding job that some readers will not supply an adequate backdrop of suffering and courage against which the art of meaningful thought has been developed. This is an excellent review of how these processes have been brought to fruition, and of how science through technology has remade the world in which we live.

The closing chapters present a stimulating discussion of the problems of applying the philosophy of science to make this better world. Chapter 15, "Determinism, Free Will and Morals," bears on that transcending problem of conflicting ideologies which has the human race by the throat today.—"The attempt to bolster the religious foundations of morals is a lost cause. If we are to enjoy again the steadying effect on human society which religious beliefs once exerted we must acquire a moral fervor for earthly values. . . . It follows that the improvement in morals will come as a result of improvement in the biological stock of the human species or in the conditions under which the human organism develops." And surely along both these lines man can use his new brain to excellent purpose, the possibilities for improvement being so extensive.

The concluding chapter on "Science and Human Values" looks briefly and stimulatingly at some of the possibilities: "Were reason both the spur and the guide to life, action would wait upon understanding, and any man questioned in the midst of his labors would be ready with an answer as to the end for which he labored." Unfortunately, this is almost universally the reverse of true. The values we live by are not very clearly defined, and the sanctions which implement these values have almost exclusively been developed in complete disregard of the fact that human beings have a mind, as well as a body and emotions. This is all of prime importance in attempting to evoke sound programs of social betterment, or of eugenic betterment. To the reviewer the conclusion of this discussion would only be modified by a stronger emphasis on the taboo and theological aspects, for the author seems to be a bit obsessed with the problem of the advertising agency rampant: "The use we make of science and the direction of social changes will not be toward the good life so long as we have an economic system in which the demand for goods which industry supplies, arises out of desire and needs which industry is able to arouse by all the subtle methods of salesmanship and advertising. The satisfactions we crave should not be foisted upon us that industry may prosper. . . . The worth of a social system should not be measured so much by the smoothness with which it runs, or by the standard of living reached in terms of consumption goods, as by the opportunity it affords its members fearlessly to employ the method of scientific intelligence in the management of their lives." Old Omar once said: "And I myself am Heaven and Hell," an aspect of evolving the Good Life, which this book, so excellent in covering part of the problem, mostly overlooks.—R. C.

*RAMSPERGER, ALBERT G. *Philosophies of Science.* Pp. xi plus 304. F. S. Crofts, New York. 1942.

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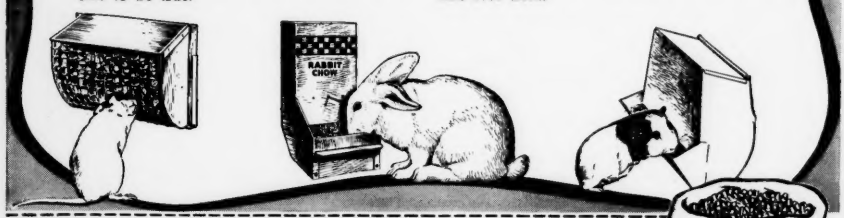

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